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MOTHS

WITH THE PUBLICATION OF *Moths*, the *New Naturalist* takes pride in one of the most important books it has offered to Britain's naturalist public, and in a major contribution to evolutionary science.

Dr. E. B. Ford, F.R.S. this book's distinguished author, wrote *Butterflies*, one of the four first *New Naturalist* volumes that set the series on its secure foundations. This new book is written in the same high scientific spirit and with the same lucidity, and is embellished with a collection of photographs by Mr. S. M. Beaufoy which, were it possible, could be held even finer than those which he contributed to *Butterflies*.

Dr. Ford's approach to his new subject, moths, is first of all genetical—which is not surprising, for he is one of the most distinguished geneticists of our day. He shows us that with moths we have a group of animals in which we can understand very deeply the inheritance of characteristics in wild populations. The study of moths thus contributes to our understanding of evolution and finds us principles which can be applied throughout the animal kingdom.

From genetics Dr. Ford leads us to the problems of distribution and dispersal, to the meaning and value of protective colouration (to which so many moths owe their incredible beauty), to economic entomology, to moth habitat, moth ecology and moth history. He ends his book with an account of the new population studies of which he is himself a pioneer.

Throughout this remarkable book runs the same sense of wonder and enjoyment that distinguished Dr. Ford's treatment of *Butterflies*. It is easy to understand why the beautiful creatures which are the subject of this book—moths—have fascinated generations of collectors and naturalists, photographers and artists, a group of enthusiasts perhaps as great as the students of birds, wild flowers, and butterflies.

It is with pleasure and confidence that we offer to the public another scholarly and scientific work by Dr. Ford.

THE NEW NATURALIST

A SURVEY OF BRITISH NATURAL HISTORY

MOTHS

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The aim of this series is to interest the general reader in the wild life of Britain by recapturing the inquiring spirit of the old naturalists. The Editors believe that the natural pride of the British public in the native fauna and flora, to which must be added concern for their conservation, is best fostered by maintaining a high standard of accuracy combined with clarity of exposition in presenting the results of modern scientific research. The plants and animals are described in relation to their homes and habitats and are portrayed in the full beauty of their natural colours, by the latest methods of colour photography and reproduction.

MOTHS

by

*E.*dmund *B.*riscoe *FORD*

F. R. S.

GENETIC LABORATORIES
ZOOLOGY DEPARTMENT, OXFORD

WITH 77 PHOTOGRAPHS IN COLOUR
71 PHOTOGRAPHS IN BLACK AND WHITE
TAKEN BY S. BEAUFOY
19 MAPS AND DIAGRAMS

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EVELYN CLARK
IN GRATITUDE FOR HER HELP
AND ENCOURAGEMENT

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EDITORS' PREFACE

The extraordinary success of Dr. E. B. Ford's *Butterflies* in the *New Naturalist* Series showed the world that there was a new wind blowing across the pastures of the British naturalists. In those early days of the *New Naturalist*, ten years ago, when the first volumes of our series were published, the Editorial Board and Publishers were inwardly convinced that books on the highest scientific level were not merely acceptable but were eagerly desired by the general reader. Now over half a million copies of *New Naturalist* books have been sold, all written by scientists distinguished in their spheres who advisedly made no effort to write down to their public but have instead written of their interest, and we may say their passion, as they might write of it to their own scientific acquaintances and colleagues.

Naturally we are all gratified that this kind of writing should have proved so readily acceptable, but we cannot say that we have been surprised. British amateur naturalists and country-lovers have proved themselves in so many ways learned and serious, and learning has fed, and continues to feed on learning. It is, then, with pride and confidence that we offer to the public another serious contribution by Dr. Ford.

As one of the most distinguished geneticists of the day, Dr. Ford's approach to his new subject, moths, is in its first part primarily genetical. And in the Editors' opinion his four great chapters on moth genetics have brought together more compellingly than has ever previously been done, the results of laboratory experiment and field observation. At last we have a group of animals in which we can understand the inheritance of characteristics in *wild populations*. Dr. Ford's synthesis advances an understanding of evolution and its principles; principles which can be applied throughout the animal kingdom, not only among those beautiful creatures which are the subject of his book.

We are led by our author from genetics to the fascinating problems of distribution and dispersal, and to the meaning and value of the protective coloration of moths, to which so many owe their incredible beauty. Wisely, Dr. Ford gives us an excursion into the realms of economic entomology, only to bring us back to the more general problems of geographical distribution (with an extremely fascinating discussion of new and little known rarities), thence to an analysis of moth habitat and moth ecology, to a discussion of moth history, particularly since the last Ice Age, and to the interesting effects of isolation. Finally Dr. Ford brings his genetical and distributional studies together in a discussion of race-formation and speciation, with a special chapter on the extraordinary phenomenon of industrial melanism; and he ends his book with an account of the new population studies of which he is himself a pioneer, studies which must have an important scientific future.

There are more than ten times as many moths in Britain as there are butterflies, so naturally *Moths* cannot do what *Butterflies* did—illustrate every species. Nobody could have expected that. But its readers will find that that able photographer Mr. Beaufoy has contributed to this book colour photographs even finer (though that is scarcely possible) than those which he contributed to *Butterflies.* The collection of plates is a most representative cross-section of British moth fauna, and figures species which are the subjects of special discussion by the author. As is *Butterflies*, this book is embellished by a set of careful distribution maps and a full bibliography.

THE EDITORS

AUTHOR'S PREFACE

This is, in effect, the second volume of a work on British Lepidoptera, of which the first, *Butterflies*, has already appeared in the New Naturalist Series. That consideration affects greatly the construction of this book, for I have assumed that readers of it are acquainted with the previous one. Indeed no other course was open to me. *Butterflies* contained a rather extensive body of information with which the majority of naturalists and collectors had previously been unfamiliar. To have repeated it in writing of Moths would have been a disastrous waste of space and tedious for those who had read it before, and they will of necessity constitute a high proportion of the public who may be interested in the present book. There is, of course, another alternative which, like so many compromises, seemed to offer the worst of two worlds. That is to say, I could have given a short summary of those subjects, such as the principles of natural selection, the elements of genetics, the structure and physiology of Insects and of the Lepidoptera, which I developed in *Butterflies*. This would have been useless to those who did not know them already, because too condensed, and dull for those who did. In this book I am therefore expanding certain of the concepts laid down in *Butterflies* and applying them, by way of illustration, to moths.

I have limited this account to the British ' Macro-Lepidoptera.' That is an entirely unjustified restriction which will be welcomed by the majority of naturalists. The Macro-Lepidoptera are an artificial assemblage, consisting of an arbitrary selection of certain families, and parts of families, without scientific validity. I have perpetuated the heresy of preserving it for several reasons. The majority of those interested in the Lepidoptera have confined their attention to the groups thus designated. These include almost a thousand species in Britain, which provide more material than is needed to display those aspects of biology on which I wish to write. The remainder, comprising the so-called ' Micro-Lepidoptera ' which are slightly the more numerous, are in general less suitable for these studies, being more difficult to handle. Moreover, they are far less well-known as to structure, phenotypic variation and distribution, and information on those subjects is often a necessary preliminary to using animal or plant material for the purposes of science and natural history.

I have throughout followed the nomenclature of Kloet and Hincks (1945) who have performed an excellent and arduous task in providing a standard list of all known British insects. Let us hope that it will not be unduly tampered with by those who seek to substitute old names for new, under the impression that they are contributing to science.

As in *Butterflies*, I have used both English and scientific names the first time that a species is mentioned in each chapter, but subsequently the English ones only. However, the latter are rarely available for subspecies and varieties, so that the scientific terminology has had, nevertheless, to be rather extensively employed. The first reference to every moth includes also the Author of its specific name, abbreviated in the usual way, and the Family to which it belongs, the characteristics of which can be obtained from the Appendix on Classification.

In choosing moths to exemplify some aspects of biology, I am of course providing opportunities for criticism. The material is so extensive and the subject so vast that however it were handled it would always be possible to point out omissions and, doubtless, errors. The errors I shall regret and hope they may not be too numerous, but with the omissions I am in no way concerned. I do not attempt to provide a complete or balanced survey of our knowledge of the British Lepidoptera, or of those aspects of science which they have been used to illuminate. I have intentionally picked merely upon a selection of them likely to interest some of those who love the countryside and study or only collect these insects. They may perhaps find added enjoyment by discovering that they can carry out useful research within the limits of their own hobby.

I have here followed and extended the line of approach which I adopted in *Butterflies*, by using moths to illustrate certain biological principles. Consequently this is no more a text-book of entomology than was the earlier volume. I have not described the species yet again, for that has been done effectively elsewhere, though I have given references to works from which such descriptions may be obtained. Nor have I given an account of the methods used in collecting moths, for such information is already and in many places available for those who want it; also I do not believe that collecting, at least in its accepted sense, is the best way of studying the Lepidoptera. It is true that I have collected myself, but I have done so merely as a means to an end. I have always been ready to destroy my specimens to examine the chemistry of their pigments, to use them in genetic experiments, or to dissect them. Entomologists would do well to follow, but greatly to extend, the methods of Ornithologists, who seldom collect but concentrate on investigating the behaviour and habits of birds: it is unfortunate that they so often fall into the usual error of Ecologists, who frequently deal with what are essentially genetic phenomena but rarely attempt to investigate them genetically.

One of the tools constantly used by bird-watchers is the photographic camera. It has been too seldom employed by entomologists, and this book demonstrates its possibilities. All the Plates, both in colour and in black-and-white, have been taken by Mr. S. Beaufoy. It has been possible to obtain them only because in him are combined the accomplished photographer and naturalist. His knowledge of our Lepidoptera, gained without forming a collection, is extensive and practical. I am greatly indebted to him both for his admirable pictures of living insects in all their stages and for the care and trouble with which he photographed the set specimens, working with me as I arranged the plates.

During the preparation of this book I have received constant help from my friend Evelyn Clark. Her encouragement, and her ability as a literary critic, have been of the highest value to me.

A number of scientific colleagues have been so good as to give me the benefit of their advice. It should clearly be understood that they are in no way responsible for the views I put forward, which are entirely my own, or the errors I have committed; but they have saved me from many mistakes and provided me with a fund of information which I did not possess and could not otherwise have acquired, especially now that my own work is principally in the fields of genetics and evolution. I wish to express to them my deep appreciation of the care they have taken and the very considerable time they have spent in helping me. I desire briefly to mention their separate contributions:

Mr. S. Beaufoy and Mrs. Edna Beaufoy have both been so kind as to read through the whole book, and their constructive criticism of it has been of great use to me. I regard myself as singularly fortunate to have received the help of Dr. E. A. Cockayne, the most experienced of all scientific students of our Lepidoptera. I have long followed his own genetic work with appreciation. He has spared no trouble in sending me detailed notes on what I have written, and these have proved invaluable. On this occasion, as so often in the past, I have greatly benefited from the sound judgment and deep biological knowledge of Dr. Julian Huxley, F.R.S. Dr. H. B. D. Kettlewell has extensive experience both of ecological and genetic work on British Lepidoptera, and I am grateful to him for reading the typescript of all the chapters and for his valuable comments upon them. I was especially glad of his help when discussing Industrial Melanism, a subject to which his researches are making notable contributions. To Dr. P. M. Sheppard, whose work as an evolutionary geneticist is well known, I am indebted for much valuable help. His studies on the Scarlet Tiger are an outstanding instance of the use of a British moth in the analysis of micro-evolution, and I am fortunate to have had the benefit of his views.

Owing to the large number of set specimens on some of the plates, it has not been possible here, as it was in *Butterflies*, to state the source from which each insect was obtained. Many are from my own collection. I am greatly indebted to Dr. E. A. Cockayne and Dr. H. B. D. Kettlewell for allowing me to illustrate numerous moths from the magnificent Rothschild-Cockayne-Kettlewell collection of the British Museum, now housed in the Zoological Museum at Tring, Hertfordshire. They have amassed an immense amount of material illustrating especially the genetics of the British Lepidoptera, which is displayed together with references to the relevant literature: an enlightened departure in Museum technique. I am fortunate to have had the opportunity of drawing upon this remarkable store; it has supplied me with the majority of the specimens demonstrating genetics and geographical variation, many of them of great rarity or interest. I am much obliged to Mr. H. C. Quelprud for the loan of numerous moths from his vast collection, also to the late Professor G. D. H. Carpenter for permission to figure specimens from the Hope Department, Oxford.

I should like to thank my secretary, Miss L. Mais, for her efficient help in preparing the typescript of this book. It presented exceptional difficulties which she overcame with skill.

Text-figures 1 to 3 have been prepared by Miss C. Court, of the

Department of Human Anatomy, Oxford. I am much obliged to her for her accurate and artistic work.

I am obliged to the Editors of *Heredity* for their kind permission to reproduce text-figures 4 to 7.

Finally, I wish to express my gratitude to the Nuffield Foundation for the financial support which they are giving to the Genetic Laboratories at Oxford. Their generosity is making it possible to study evolution experimentally, by a combination of work in the laboratory and in the field. Some of the results thus obtained, both by my colleagues and by myself, are described in this book.

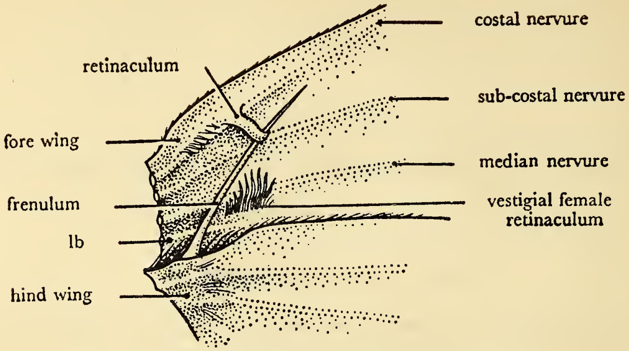
CHAPTER I

STRUCTURE AND PHYSIOLOGY

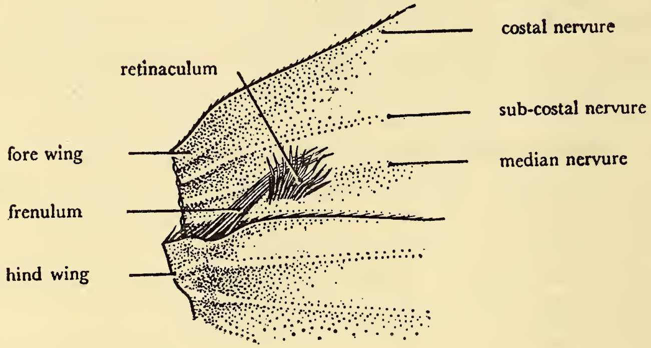
Moths and Butterflies

THE MOST IMPORTANT THING to remember about moths is that they are insects, whose organisation, with its strange advantages and drawbacks, affects profoundly the structure and working of their bodies. Because of the way in which they breathe they are small and could be no larger, in the sense that some have attained the maximum possible size, and this is both an advantage and a handicap to them. Their blood has direct access to their tissues, a system effective for the transport of material but dangerous in the event of injury. They are very susceptible to desiccation and must guard against it by a series of devices affecting both their excretion and respiration; while their eyes are complex, but rather inefficient, organs of vision. These facts have been explained, and the anatomy and physiology of the Lepidoptera described, in *Butterflies* (Chapters 2 to 4), and it is here necessary only to indicate those features of structure and habit by which moths differ from the rest of the Order.

The characteristics of each of the families that are, by strange convention, included in the Macro-Lepidoptera (page xv) are given in the Appendix on pages 231-8. The neuration of the wings varies so much from one group to another that it does not provide a valid distinction between butterflies and moths. That is generally supplied by the coupling device which holds the fore and hind wings together during flight. In most moths this takes the form of a spine, the *frenulum*, which arises from the base of the hind wings. It is single in the male but multiple, though probably weaker, in the female. It fits into a catch, the *retinaculum*, on the underside of the fore-wings, constructed very differently in the two sexes. In the male it consists of a strap-like flap of chitin arising from the costal nervure. The free end is directed backwards and turned up towards the wing, so holding the *frenulum* in place. In the female the *retinaculum* is formed by a row of


costal nervure
retinaculum
sub-costal nervure
fore wing
median nervure
frenulum
vestigial female retinaculum
lb
hind wing

MALE UNDERSIDE


costal nervure
retinaculum
sub-costal nervure
fore wing
median nervure
frenulum
hind wing

FEMALE UNDERSIDE

FIGURE 1

The apparatus which unites the fore and hind wings of a moth during flight

stiff bristles along the median nervure and is therefore nearer the centre of the fore-wings. The *frenulum* engages in front of this. A vestige of the female arrangement is generally present in the male, in which also some bristles usually arise on the basal side of the strap-like *retinaculum*. The arrangement as present in the two sexes is shown in text-figure 1, while the *retinaculum* of the male is strikingly displayed in Mr. Beaufoy's photograph of the Puss Moth, *Cerura vinula* L., Notodontidae, on Plate III, figure 1. In many species the type of *frenulum* and *retinaculum* provides the easiest method of distinguishing males from females.

A different system is employed by the Hepialidae, the 'Swift' Moths, consisting of a small flap, the *jugum*, which arises from the inner margin at the base of the fore-wings. It overlaps the hind-wings and presumably helps to ensure that the two pairs beat in unison, though it does not seem a very efficient means of doing so. These coupling devices are absent from a few moths; for instance, the Lasiocampidae and Endromididae. The wings of butterflies, on the other hand, are united in flight by a *humeral lobe*, a projection from the hind-wings which passes forwards beneath the front pair. A *frenulum* is retained, however, by one genus of the Hesperiidae, the "Skippers." This is the Australian *Euschemon*. Since it possesses many primitive characteristics, it is clear that this structure was invented at an early stage in the evolution of the Lepidoptera and lost in the Papilionidae.

The *antennae* of butterflies are never feathered or 'pectinated'; moreover, they always end in a knob while those of moths rarely do so and never in the forms without the *frenulum*. Thus it comes about that these two features, the wing-coupling apparatus and the shape of the antennae are, when considered together, a sure distinction between the two groups.

The development of the wings in the late larva and in the pupa, and the way in which they expand when the perfect insect emerges, has been described and rather fully illustrated in *Butterflies*. Three stages in their expansion in a moth, the Pale Tussock, *Dasychira pudibunda* L., Lymantriidae, are shown on Plate III, figure 2-4. That process is depicted again in this book in order to demonstrate a curious feature not apparent in the emerging Red Admiral (*Butterflies*, Plate VI). The majority of moths hold their wings flat (Plate VII, figure 6), but sometimes outspread or wrapped around the body (figure 4). However, in all butterflies except some of the Skippers (Hesperiidae*) and in many moths belonging to the families Hydriomenidae, Selidosemidae and some others, the wings are carried raised over the back (figure 5). This is a "fixation" from one of the stages during their normal expansion, for in all species they are for a time raised in this way in order to dry, as shown in Plate III, before being brought down to their normal position (figure 4).

*Also some tropical Riodinidae.

The undersides of the wings usually bear an elaborate colour-pattern in those moths which expose them when at rest. They are dull-coloured in those night-flying forms which sit with them concealed; but in the day-flying species which do so they are often of striking appearance, as the lower surface of the wings is visible when the insect flies.

No species of moth seems to have reverted to the wingless state in both sexes, though some have done so in the female only. The reason why the males of these insects retain their wings is discussed in Chapter 6. This apterous condition has been independently acquired in several groups and, since it is generally present in a few of the species only, it is better mentioned now than in the Appendix on Classification.

Wingless females occur in three families of the British Macro-Lepidoptera: the Lymantriidae (two species), the Hydriomenidae (two species) and the Selidosemidae (nine species). In the majority of them the wings of the female are reduced to little flaps two millimetres or so in length (for instance, the Belted Beauty, *Nyssia zonaria* Schiff., Selidosemidae, Plate XIII, figure 7). They may, however, be so short as not to protrude beyond the scales clothing the body, so that the insect appears completely apterous (as in the Mottled Umber, *Erannis defoliaria*, Cl., Selidosemidae, Plate XVIII, figure 2), while at the other extreme they are large enough to have a distinct, and variable, colour-pattern, being about a quarter the length of the functional wings of the male (The Dotted Border, *E. progemmaria* Hb., Plate XVIII, figure 3 male, 4 female). Some females never fly, though they have wings large enough for the purpose; for example, the Gipsy Moth, *Lymantria dispar* L., Lymantriidae, Plate 32, figure 3 male, 4 female, in some but not all of its forms, the distinction being genetically controlled. This is evidently a step towards their total loss, and it is worth noting that the Gipsy belongs to the same family as the Vapourer, *Orgyia*, in which the process is carried much farther (Plate 1, figure 1). When species with winged and wingless females have been crossed in the laboratory the female hybrids have had wings of about one-third of the normal area (Plate XIII, figures 11 and 13); probably the difference is multifactorial (pages 54-5).

The colours of moths are produced by similar means to those of butterflies, described in the previous volume (*Butterflies*, pages 57-61), for they also may be structural or pigmentary. Structural colours are the result of ' interference ' phenomena, as are those on a soap-bubble.

They arise when the scales are built up of a number of layers separated by a material of a different refractive index. They may also be due to diffraction, if the surface bears minute ridges. Most of the blues are produced in this way; so too are the more metallic types of green, such as that of the green Foresters, Zygaenidae (Plate 26, figure 11). Consequently, when their wings are moistened, as they can be with a fat-solvent, chloroform for instance, but not with water, the green disappears in a Forester but not in an insect in which it is due to a pigment, as in the Geometridae (Plate 1, figure 4). Blue is an exceedingly rare hue in moths, while green is much commoner than in butterflies though still unusual.

I have made rather detailed studies of certain pigments in butterflies, but have attempted nothing on such an extensive scale in moths. In the latter group, the type built up from uric acid is so far unknown, for among the Lepidoptera it appears to be restricted to, though universal in, the Pieridae (the White and Sulphur butterflies and their allies). Similarly, flavones have not yet been detected save in certain butterfly genera; but though these are relatively few in number they are so widespread that there seems a reasonable prospect that these substances occur also in moths. They are non-nitrogenous, and range in colour from ivory to deep yellow. Flavones are never manufactured by animals but are derived from the plants upon which they feed.

There is a type of red pigment widespread in the Lepidoptera which is easy to recognise but difficult to study chemically; indeed, I believe it has never yet been satisfactorily analysed. It does not give a murexide reaction, which is the test for uric acid and some of its derivatives, and is but very slightly soluble in hot water. However, it is with great rapidity converted to a bright yellow shade by an acid (*e.g.* hydrochloric) and restored to red again by an alkali (*e.g.* ammonia), a treatment that does not damage the specimen. This is the substance responsible for the red colours of the Tiger Moths (Arctiidae and Hypsidae, Plates 9 and 11), the Red Underwings (Plusiidae of the genus *Catocala*, Plate 5) and the Burnets (Zygaenidae, Plate 8). Alternative yellow varieties or forms are found in every species in which it occurs (Plates 8 and 9), and perhaps the yellow compound is a stage in the production of the red. It is probably the most widely distributed of the six red pigments so far identified in butterflies, but it is not present in any of the British species.

I find that the green pigmentary colours of moths are of two types.

Though neither is produced by unaltered chlorophyll, it is likely that both are derived from that substance. One, that present in the Emerald Moths, Geometridae (Plate 1, figure 4), is changed to a reddish-brown shade by an acid: the green coloration cannot then be restored by subsequent treatment with an alkali. The other form is uncommon but rather widespread; it is found, for instance, in the Green Silver-lines *Bena prasinana L.* (Plate 16, figure 1) and its allies, the Cymbidae, and in some Sphingidae such as the Oleander Hawk, *Daphnis nerii* L. It temporarily becomes slightly bluer in tone on exposure to an acid and is converted to a brown shade by an alkali. However, this change is to some extent reversible, for the green can be recovered, at least partially, by an acid, which will restore some of the beauty of youth even to old brown specimens long preserved in collections. In order to retain their colouring, green insects of this kind should be killed with potassium cyanide, which is always somewhat acid, while the Emeralds should be killed with ammonia.

Some of the yellow pigments of moths, as of butterflies, are brilliantly fluorescent in ultraviolet light, and they can be extracted with alcohol, producing fluorescent solutions. They occur, for instance, in the Brimstone, *Opisthograptis luteolata* L., and the Swallow-tailed Moth, *Ourapteryx sambucaria* L., both Selidosemidae, though they are chemically different in these two insects, a fact not previously reported. If a specimen of each of them, together with an ordinary White Butterfly, be exposed to ultraviolet light passed through Wood's glass, which cuts out nearly all the visible range of the spectrum, the ' White ' will be dimly perceptible as a blackish-brown object, while the two moths glow brilliantly with a yellowish phosphorescent light.

The distribution of these pigments should be more thoroughly studied, especially in moths, and related to classification, on which it sometimes throws considerable light. Some of the tests by which these substances can be recognised are quite simple (Ford, 1941, '42, '47) and such an investigation would be a delightful task; for it is one that could be undertaken by anyone interested in this type of problem even if he were by no means a proficient chemist.

Hardly anything is known about the pigments of larvae and pupae, though doubtless the majority of them are of the same types as those occurring in the imagines. Indeed in the American butterfly *Colias philodice* Godt., Pieridae, the larvae, pupae and eyes of the imago are normally green, but a recessive mutant form is known in which they are bright blue. Since this affects all the stages, it is likely that the same pigment is involved throughout.

The anatomy of larvae and pupae and the formation in them of imaginal buds, giving rise to the structures characteristic of the imago, have been described in *Butterflies*, Chapter 2. Consequently it is necessary now only to draw attention to a few minor features not mentioned in that account.

Some larvae not only change their colour-pattern as they become larger (Chapter 7) but alter their proportions, because their parts do not grow at a uniform rate. Huxley (1932) has made a detailed study of such "allometric growth." It can be described by a simple formula of the widest application. If y be the size of any organ of the body, estimated in terms of length, weight or any other suitable measurement, and x that of the body minus the organ in question, then the relation between them is:

$$y = bx^{\alpha}$$

where b denotes the initial relationship, being the value of y when $x = 1$, while the term α, known as the relative growth-coefficient, describes the ratio of y to x; that is to say, if $\alpha = 1$, organ and body retain their proportions. Growth is then *isogonic*, and the animal maintains its original shape so far as this particular structure is concerned. If α be greater than 1, the organ in question becomes disproportionately larger during growth, while if α be less than 1 it fails to keep pace with increasing body-size; in fact it becomes absolutely larger but relatively smaller. When α is not unity, growth is said to be *allometric*. Huxley established that instead of being unstable, α is generally constant throughout long periods of the life of the organism, though it may alter at some critical period such as sexual maturity. Consequently if the logarithms of x and y be plotted, the resulting graph is a straight line, from the slope and position of which α and b can be deduced.*

The numerical values concerned are often of biological interest since considerable apparent differences between related forms are sometimes due to no more than simple changes in the constants b or α. However, it is only necessary here to note that allometric growth allows larvae to alter their shape during the course of their lives, for proportions that are suitable at one size may not be appropriate at another. Thus many larvae have fantastic horns and excrescences when small.

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*If θ be the angle which the line makes with the x axis, $\alpha = \tan\theta$, while the point at which the graph meets the y axis $= \log b$, from which b may be found.

These perhaps help to conceal their shape, and they may become progressively reduced as the creature grows and acquires other protective devices such as a different colour-pattern, or perhaps an offensive smell which might not be effective in a very small creature. Such changes are illustrated by the larva of the Poplar Hawk, *Laothoe populi* L., Sphingidae (Plate IV, figures 2 to 4). It will be seen that the posterior horn is relatively immense soon after hatching (figure 2), being about a third the length of the body, and that its size is progressively reduced during growth, becoming in the end a very minor feature of about one-tenth the body-length (figure 4), owing to the fact that, in respect of this structure, α is less than unity. There are, of course, other instances in which structures become more accentuated during larval life because the value of α in their growth-formula exceeds 1.

The early stages of moths are in their general features similar to those of butterflies, while the chief forms which they assume in the various groups are described in the section of Classification. However, the pupae of butterflies are exceptional, so that it is necessary at the outset briefly to mention certain characteristics of the more generalised types found among moths. On the whole, the evolutionary trend of Insects has been to mark off the pupal and larval states more sharply from one another. In primitive Lepidoptera the pupa is still somewhat larval in appearance, as in the Hepialidae (Plate IX, figure 1), while in the more highly evolved groups it acquires a distinct shape, with an inflated thorax and relatively narrow abdomen, as in the Selidosemidae (Plate XVII, figure 1). That of the Privet Hawk, *Sphinx ligustri* L., Sphingidae, and of a few species closely related to it, shows a feature not observable in butterflies; for the case containing the proboscis is not in contact with the body throughout its whole length (Plate VIII, figure 1), showing that it is a separate structure which is merely glued down to the surface. This, of course, is true also of the wing- and leg-cases, though normally no part of them is free.

The pupae of nearly all moths are enclosed in some form of cocoon: a structure which the butterflies have lost except for the Skippers, Hesperiidae. Consequently it was discussed but briefly in the previous volume and a more detailed account of it is needed here. It was pointed out, however, that the silken girth which supports the chrysalis head upwards in certain of the less highly specialised butterfly families probably represents the last vestige of a cocoon (*Butterflies*, page 85).

The pupa of many moths, as of a few butterflies, is subterranean and lies in a cavity excavated by the larva. The walls of this chamber are hardened by a larval secretion, and sometimes lined by silk, to prevent their collapse (the Merveille du Jour, *Griposia aprilina* L., Caradrinidae (Plate VIII, figure 3). The imago must then force its way up through the soil on emergence. Usually such pupae are buried no more than an inch or two, but those of the large Hawk Moths may lie four or five inches below the surface.

Some species spin a cocoon of silk and leaves, rather like that of the Skipper butterflies (the Large Thorn, *Ennomos autumnaria* Wern., Selidosemidae, Plate XVII, figure 1). Those which feed internally, boring into trees or stems of plants, often pupate in the mines excavated by the larvae. Here they form a chamber by closing off the gallery on either side of the pupa by a plug of silk interwoven with fragments of food (Plate XVII, figure 4, which shows the Bulrush Moth, *Nonagria typhae* Thnbg., Caradrinidae).

There are some groups in which the cocoon is constructed entirely of silk. It may be loose and fluffy as in the Gold-tail, *Euproctis chrysorrhoea* L., Lymantriidae (Plate IX, figures 3 and 4), firm and papery as in the Zygaenidae (Plate 24, figure 5, the Six-spot Burnet, *Zygaena filipendulae* L.), or hardened by the larval secretion and by the inclusion in it of fragments of wood (see Chapter 7). The latter type is usually placed on branches or tree trunks, and is very well concealed; that of the Waved Umber, *Hemerophila abruptaria* Thnbg. Selidosemidae (Plate XVII, figure 2) provides a good example of this kind. Some silken cocoons are double or even triple, with a fluffy exterior and a harder inner shell: a famous instance of them is that of the Silk Moth, *Bombyx mori* L. (page 101), but our own Pale Tussock, *Dasychira pudibunda* L., Lymantriidae, and some other British species, have a double cocoon. This is doubtless protective, the soft loose outside perhaps discouraging insectivorous birds and the harder inner layer preventing the entrance of parasites. In general, cocoons, especially those largely composed of silk, are a safeguard against damp and mould.

Scents and the Sense of Smell

A few moths in some or all of their stages are known to produce scents which are presumably protective because unpleasant. The larva of the Goat Moth, *Cossus cossus* L. (Plate 6, figure 1), and that of the Buff-tip, *Phalera bucephala* L., Notodontidae (Plate 21, figure 3) are examples of them. It is likely that the device is a common one, but our own olfactory powers are so weak that it generally passes unnoticed. I am not aware that the glands which manufacture such scents have been discovered. Probably they take the form of cells scattered over the surface of the body.

All the scent-producing organs in moths that have been studied in any detail are connected with courtship, and they are of two principal types: those produced by the female to attract and direct the males to her, and those produced by the male to induce the female to perform the sexual act. Both are perceived by the antennae, on which are situated great numbers of " end-organs " capable of being stimulated by volatile substances, the " scents " carried in the air. There are several types of these structures, but in general, they are minute cups on the chitinous surface, in the centre of which is a projection connected to a nerve cell. The antennae of females are relatively simple, for they are chiefly engaged in registering the aphrodisiac scent of the male produced near at hand when he has reached her. Thus they consist of jointed rods, only occasionally provided with short side-branches. Those of the males, however, are in some species much more elaborate with brush-like extensions along both sides so that their surface is greatly increased. It is necessary that it should be so since they are called upon to perform one of the most surprising feats of perception achieved by any animal; for some species of male moths, notably the Eggars (Lasiocampidae) and Lymantriidae, respond to the attractive scent of a female a mile or more away. This must mean that their olfactory organs are capable of effective stimulation by single molecules. Moreover, their response is highly specific: the males will fly from the country into a town, with its manifold smells, in order to reach a female, and into a room filled with the reek of tobacco smoke.

Males, of course, " assemble " or fly to females only upwind, and they gauge the direction by contrasting the number of molecules striking each antenna per unit of time. Consequently specimens which have lost one antenna perceive the scent of the female but fail to find her accurately, while those which have lost both antennae are incapable of assembling. There must be considerable loss of the female scent in hot sunshine, when convection currents carry much of it upwards rather than outwards. It is not surprising therefore that most moths assemble at dusk or dawn when there is generally a layer of cool air on the surface of the ground. Moreover, the scent-substances of the females, probably always volatile oils, will vaporise slowly in cold conditions. Kettlewell has examined the antennae of males belonging to the rather exceptional species which assemble in sunshine or in the cold months of the year, and finds some tendency for them to possess unduly long side-branches (" pectinations "), so increasing their area.

The attractive scent of the females is produced by glands at the posterior end of the body. These are under " voluntary " control. When a moth is " calling " she extends the last segments of her body, which pulsate rhythmically at about 60 cycles per minute. Only in these circumstances does she elaborate her scent, and only then do the males assemble to her. A detailed study of the female scent of the Gipsy Moth, *Lymantria dispar*, has been made in America. This can be extracted in benzine and the solution stored at 35° F. It was in fact used commercially to attract and destroy the males, for this species has become a pest in the United States, where it was accidentally introduced. It was found that hydrogenation of the extract, by shaking with hydrogen in the presence of platinum oxide as a catalyst, increased its attractiveness. The substance proved to be a volatile oil with a molecular formula of approximately $C_{27}H_{46}O$. It was not possible to manufacture it synthetically.

Objects, such as a box or a net, which have been in contact with a female moth when producing her scent become attractive to the male. They, of course, remain so for varying periods of time according to the species and the temperature. Kettlewell found that the scent of the Emperor Moth, *Saturnia pavonia* L., disappeared very rapidly, while that of the Grass Eggar, *Lasiocampa trifolii* Schiff., might still be effective seventy-two hours after it had been produced.

Large numbers of males often fly to a single female. It is clear therefore that the act of assembling is highly competitive, and selection must strongly favour a well-developed sense of smell.

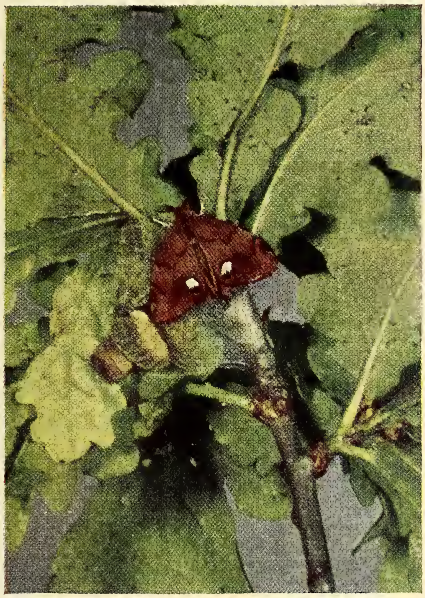
As might be expected, the range of substances suitable to act as the attractive scents of female moths is apparently rather limited, so that several species use the same: for instance, the Wood Tiger, *Parasemia plantaginis* L., and the Cream-spot Tiger, *Arctia villica* L., the Ruby Tiger, *Phragmatobia fuliginosa* L. (all Arctiidae), and the Scarlet Tiger, *Panaxia dominula* L., Hypsidae. Other instances of a similar kind have been reported. The time of day at which assembling takes place is different for these species, and remarkably constant for each, so that the use of the same attractive substance is not prejudicial to them. (For those who require a more detailed account of assembling scents, I recommend the excellent article by Kettlewell, 1946.)

We know even less of the scents by which males stimulate the sexual activities of females, and the subject has been more fully studied in butterflies than in moths. In the latter group, various scent-glands and brush-like organs for distributing the volatile substances have been described, particularly by the late Dr. H. Eltringham. One of the best known of these structures occurs in various Caradrinidae such as the Dark Arches, *Xylophasia monoglypha* Hufn., and the Angle-shades, *Phlogophora meticulosa* L. In the males of these species may be found a long narrow pocket in the cuticle of the abdomen, starting in the first segment and running along either side for about six millimetres. It is slit-like and, having the edges pressed closely together, is rather difficult to see. Inside it is housed a brush which can be opened fan-wise by muscle-fibres. This is composed of very numerous long narrow scales up each of which penetrates a minute tube from a gland-cell at its base. It is evidently a distributing organ for the stimulating scent of the male, presumably used when flying in proximity to a female. A specimen of the Angle-shades with the brushes extended is shown on Plate II, figure 2: it is seen from below.

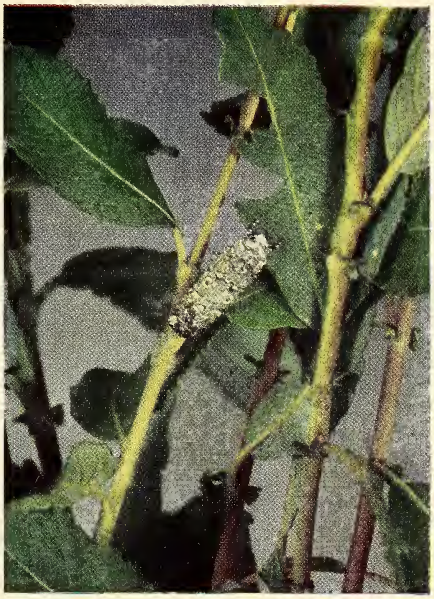
I find that very few collectors have examined their specimens for these and similar organs. Indeed it is surprising how little experimental work has been done on the scents and extraordinary olfactory powers of moths. The subject would repay the attention both of entomologists and chemists.

HEARING

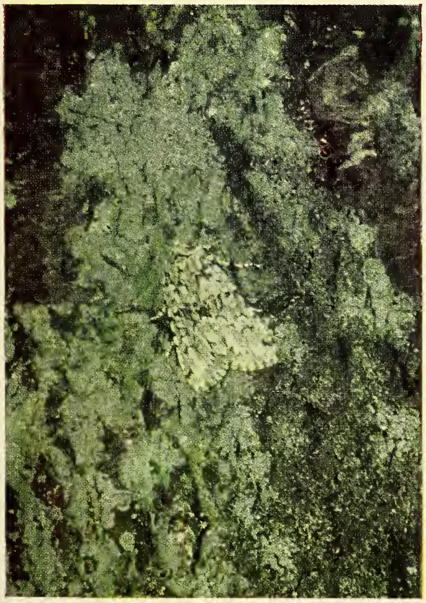
It has already been pointed out in the previous volume of this work that butterflies are sensitive to sound, although they never possess paired "tympanic organs" such as are found in certain moths. Though large enough when well-developed to occupy the greater part of a segment, these structures vary in their position and occurrence among the Lepidoptera to an unexpected extent. They are situated in the metathorax in many groups, such as the Caradrinidae and Lymantriidae, but in the first abdominal segment of the Hydrio-



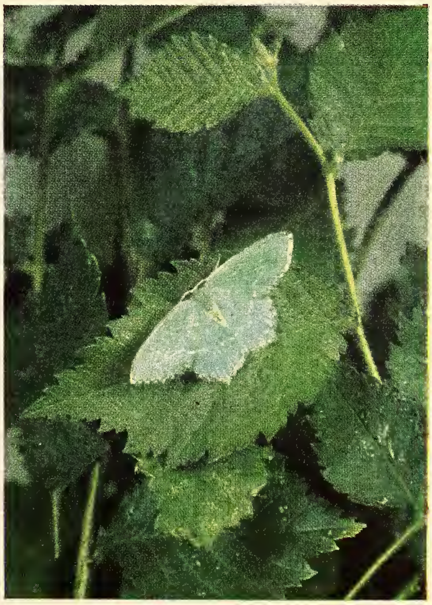
1. Vapourer, *Orgyia antiqua*, male and female



2. Portland Moth, *Actebia praecox*

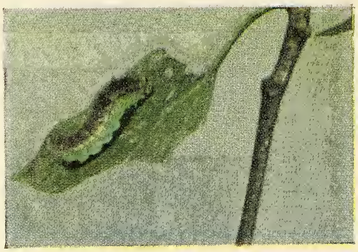


3. Merveille du Jour, *Griposia aprilina*

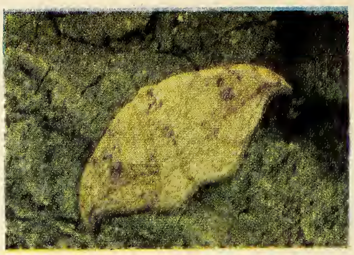


4. Common Emerald, *Hemithea strigata*

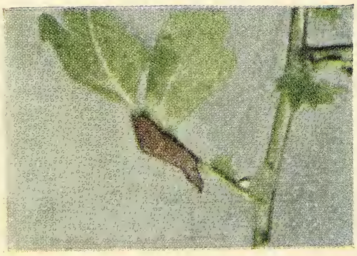
Plate 1. Deceptive and Cryptic Colouring
(Portland Moth slightly reduced)



1. Pebble Hook-tip, *Drepana falcataria*, larva

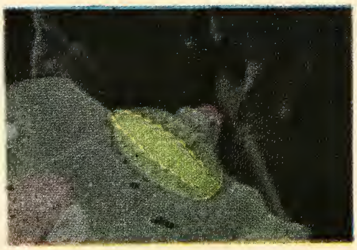


2. Pebble Hook-tip, imago

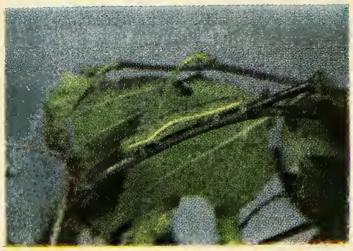


3. Chinese Character, *Cilix glaucata*, larva

4. Chinese Character, imago



5. Festoon Moth, *Cochlidion avellana*, larva



6. Orange Underwing, *Brephos parthenias*, larva

Plate 2. MOTHS AND THEIR LARVAE

menidae, Selidosemidae and others: while they are absent from the Sphingidae, Hepialidae, and, as already mentioned, from Papilionoidea (butterflies).

Tympanic (or hearing) organs consist of an ear-drum usually situated in a pocket on the side of the body. This is easily seen in the preparation of the Swallow-tailed Moth, *Ourapteryx sambucaria* L., Selidosemidae, shown on Plate I, figure 1, in which the scales covering the entrance to it have been removed. The drum is a thin membrane of chitin stretched across a firm ring of the same material. Behind it are one or more tracheal spaces, allowing free movement. Sense-organs with nerve-fibres run to the centre of the drum and record its vibrations. A model of the structure, made by the late Dr. H. Eltringham, is illustrated on Plate I, figure 2. It is arranged as if the body of the insect had been cut through transversely in front of the " ears." The large white rods rising vertically together are a pair of nerves originating from the ventral nerve-cord, which can be seen cut across at the base.

There is good evidence that these tympanic organs are sensitive to sound. Many moths vibrate their wings or fly in response to high-pitched notes but do so no longer if the ear-drums are damaged. It is not certain, however, that this is their only function. In some species they may also respond to changes in pressure, so possibly checking the tendency to ascend farther when the insect has reached a considerable height (Chapter 6). Indeed if the sack behind the drum is connected to the exterior only through the finer branches of the tracheal tubes, the tympanic organ would be well fitted to act as a barometer; as to some extent can the human ear, a fact which will have been noticed by all who have ascended or descended rapidly in an aeroplane. It is indeed well known that environmental stimuli may evoke such changes in behaviour. For example, many newly-hatched larvae automatically crawl upwards until after their first meal, the digestion of which annuls the tendency to do so; this being an adaptation to ensure that they climb to the leaves of their food plant and to enable them subsequently to wander from one branch to another.

SIGHT

The compound eyes of the Lepidoptera are of intricate design and relatively large size, occupying the greater part of the head (Plate II, figure 1). They have been described in *Butterflies*, Chapter 3, where an account is given both of their structure and the way in which they work. Thus it is necessary here only to discuss one aspect of visual response especially characteristic of moths, the tendency to fly towards a light. This reaction has always aroused interest, and collectors have long used it as a method of obtaining their specimens. The devices employed are various: the insects are attracted into lighted rooms, to portable illuminated traps with glass fronts so arranged as to make entrance easy and exit difficult, to lamps taken into the field and used alone or shining on to a sheet, and to motor-car headlights. It is only in recent years, however, that this curious reaction to a stimulus that is so largely, though not entirely (Chapter 6), a product of civilisation has been investigated in detail, first by Williams (1939) and later by Robinson and Robinson (1950) who have devised a new technique for its analysis. This has enabled them to determine the type of illumination which is most effective and to study the behaviour of moths under its influence.

Robinson and Robinson find that if the power of a light-source, measured in lumens, be increased, the number of insects visiting it is increased also, and approximately in direct proportion; yet the number of distinct species that arrive remains the same. That is to say, those species flying in the immediate neighbourhood which are not attracted to a light of a given power fail to be attracted however greatly that power is intensified, provided it retains the same surface brightness expressed in lumens per square centimetre (which can happen if its power and area be increased proportionately).

An increase of surface-brightness, on the other hand, ensures, in approximately direct proportion, an increase in the number of species visiting the light. It does not, however, attract a greater total number of insects when allowance is made for the new species arriving.

Since the surface-brightness of a lamp is its power divided by its surface-area, the most efficient type for attracting moths is one with a very high power but very small source of illumination. Various designs tending to combine these features are available but the majority of them have serious defects on the score of expense, mechanical difficulties, or shortness of life, and the Robinsons find that the most practical is the medium-pressure mercury-vapour discharge lamp.

Two of the properties of a light-source, power and surface-brightness, have so far been mentioned; a third is spectral content.

The ranges of radiation to which the eyes of insects and of men respond, which in fact they see, are not the same, though they overlap; for the perception of insects is shifted to somewhat shorter wave-lengths (approximately 2,500 to 6,300 Å) compared with our own (approximately 4,000 to 7,800 Å), so that they see into the ultra-violet but not so far into the red.

If the light from a mercury-vapour lamp be passed through Wood's glass, the radiation which emerges is almost entirely in the ultra-violet field. It represents 70 per cent of the total output visible to an insect but only 2 per cent of that visible to a man. Thus it is possible to attract moths to a lamp that to our eyes is virtually without light and is black. Indeed, owing to the high power and surface-brightness of a mercury-vapour lamp, such a source may provide a more efficient means of collecting than an ordinary light. It is a curious experience to enter a dark room to which moths are being attracted in hundreds and to switch on an ordinary electric bulb and find the insects flying to the " invisible " rather than the " visible " light.

Very little work has so far been done on ascertaining the wave-lengths that are especially attractive to moths, but such information as exists does not indicate that species vary considerably in the extent to which they are stimulated by different parts of the range perceptible to them. However, some birds are defective in their appreciation of the blue end of the spectrum. On the other hand, Dr. R. Rensch and I, when in the subtropical rain forest of Queensland, examined the reaction of a Bower-bird, *Ptilonorhynchus violaceus* Vieill., which decorated its playground with bright blue objects, the flowers of a blue *Solanum* and the blue feathers of a parrot. I am prepared to find analogous types of variation among moths, some species of which may perceive wave-lengths beyond the range appreciated by others.

Robinson and Robinson point out that the response of moths to radiation is far from being a simple attraction; for many of the insects approach to within a certain distance of the light, about a hundred feet from a hundred-watt filament lamp, partly circle it and then fly away. Others on reaching the same distance vacillate in their course and then approach the light in a logarithmic spiral curve. They seldom strike it, but rather pass and repeat the process or fly round the source in a narrow circle of about a foot in diameter. These authors accordingly suggest that a light is the centre of two concentric spheres of effect. The larger, or sphere of repulsion, extends to the distance at which the insects become affected by the light; the smaller, within it, is a sphere of dazzle. Any moths which enter this are deflected in their course so as to pass near the light, perhaps because of a failure in optical adjustment to the brilliant illumination, like the effect of dazzle on Man.

If, so it is argued, an insect in the course of its flight passes into the outer sphere it will tend to avoid the lighted area and alter its course accordingly. Only if its velocity carries it through to the region of dazzle will it approach the light. This will often happen if its " avoiding reaction " is slow or if the inner sphere is not much smaller than the outer.

The size of the outer sphere is a function of the power of the light, while that of the inner one depends on the dazzle effect. This is due to the contrast between the light and its background and must increase with the surface-brightness of the source. The Robinsons point out that owing to the interference between the different concentric spheres of neighbouring lights, the closer illuminants are clustered together the smaller will be the number of insects that reach them. It is for this reason that single lights in the country attract moths more effectively than the multiple ones at the edge of a town. There can be little doubt that this general interpretation entails a large element of truth, though it may be questioned if it is correct in all details.

As a result of their findings, the Robinsons have elaborated a new and remarkably effective moth-trap. This consists of a medium-pressure mercury-vapour lamp (one using 125 watts was found satisfactory) set at the centre of eight radial vanes twenty-four inches in diameter which intercept the flight of the insects so that they "stall" and fall into a cylinder below, containing tetrachlorethane vapour. The amount of this substance being vapourised can be accurately controlled so as to anaesthetise the specimens without killing them; thus they can be examined subsequently and liberated.

The efficiency of this device is indicated by the fact that such a trap, working on a single night in Hampshire, collected more than 50,000 specimens of the Setaceous Hebrew Character, *Amathes c-nigrum* L., Caradrinidae, and vast numbers of other species. Indeed it is revolutionising the capture of moths and, as a result, our present knowledge of their distribution may well prove to be very defective. It is now being shown that some species long thought to be rare are abundant, and that others exist where they have never before been recorded.

Finally, one aspect of these results deserves special mention here. It had long been thought that light stimulates the two sexes very unequally, males alone or to a predominant extent being attracted. This proves to be false, for the two sexes are apparently equally affected in all species. When one only is taken, it indicates a sexual difference in time or place of flight. Two features have in the past contributed to give the impression that males visit a light very much more than do females. First, the latter sex usually flies only after mating and then only between periods of egg-laying, while the males are constantly searching for females and available for capture. Secondly, males fly higher than females, so that a larger proportion of them is caught in raised positions and at upper windows, which are often used as moth-traps so as to obtain a wide and uninterrupted field of illumination. This difference in behaviour may be associated with the distribution of the hereditary material rather than of individuals. A discussion of it must therefore be postponed until the section on Dispersal (pages 87-9), when it can be considered in relation to the account of Genetics given in the intervening chapters.

CHAPTER 2

GENETICS

Introduction

It has been pointed out in the Preface that this is virtually the second volume of a work upon British Lepidoptera, of which *Butterflies*, already published in the New Naturalist Series, is the first. Consequently a knowledge of the technical terms and principles explained in that book is presumed in this one: a matter of much importance in the present and three following chapters, which are devoted to genetics. For they would be incomprehensible to anyone who approached them without previous guidance, but it will be found that they follow naturally from the account given in *Butterflies.*

There are very few subjects in which the amateur can so easily and inexpensively make substantial contributions to scientific knowledge as in genetics, and particularly in the genetics of butterflies and moths. He can do so without disorganising his hobby or indeed very much extending it, even if his previous aim has merely been to amass a collection. He need only systematise his breeding of insects, keep his broods rigorously separate, and record his results accurately in the light of Mendel's laws and a few elementary extensions of them. Moreover, these are so simple that I have known a child of eleven master them in an afternoon and successfully apply them, without help, to the combination of different varieties of tame mice.

When a gene not previously recorded is detected in the course of breeding from varieties, the information should be published. Special attention should be paid to those instances in which the results are difficult to analyse or unexpectedly complex. In such circumstances, the advice of a geneticist should be obtained.

Some of the situations especially worth studying will be illustrated by the examples given in this and the following chapters. No attempt will be made to list all the genes so far known in moths. That is a task for specialist literature. It is one which I myself attempted in 1937, and there is now a great need for that article to be brought up to date. But a book in this Series, which is devoted to a general survey of natural history, in its wider and more modern sense, is certainly not the place to do so. Here I shall merely illustrate a number of genetic principles by examples chosen from British moths. In addition, I shall draw attention to those aspects of the subject which have been neglected in the Lepidoptera, in the hope that entomologists and collectors may be able to supply the data on them which are so badly needed.

Here I would introduce a word of caution. No attempt should be made to use material for purposes for which it is ill-adapted. That is one of the dangers of concentrating on *groups* of animals or plants, rather than on biological *problems*. The entomologist or ornithologist thinks in terms of insects or birds. That was the right way to think when biology was being developed in the past: it is becoming the wrong way to think to-day. It is quite reasonable, as far as possible, to use for study or experiment those organisms which we know how to handle and with whose habits we are familiar, but we must not be limited by them. An instance purposely chosen as remote from the subject in hand, and therefore illustrative only, is provided by the work of the distinguished Danish geneticist Øjvind Winge. He had long been breeding fish, especially *Lebistes*, not as an ichthyologist but because they supplied suitable material for the analysis of sex-determination. Rightly enough he therefore employed *Lebistes* in that work so long as it served his purpose, but at one stage he found that flowering plants, *Melandrium* (Campions), *Humulus* (Hops) and others, rather than fish, provided the key to his problem, and to flowering plants he accordingly turned. We may wonder how many entomologists would have done the same.

One can put the matter in another form. If we are to confine ourselves to butterflies and moths it is best to restrict our attention to those aspects of genetics, and there are many, which can be studied particularly well in those insects. On the other hand, the chromosomes of the Lepidoptera are on the whole small and numerous: thus they do not provide good material for the investigation of chromosome structure or indeed for work upon the physical basis of heredity. Consequently, the moth-collector whose interest in genetics has been aroused need not feel that he should master the delicate techniques of cytology: which, indeed, can hardly be attempted without the facilities of a scientific laboratory. On the contrary, the simple apparatus he is likely already to possess will, if rightly used, be sufficient for his needs.

It is unnecessary to give any detailed advice here on the breeding of butterflies and moths. Information on types of cages, the sleeving of larvae, and the care of pupae is available in many places. A few comments are desirable on one aspect only of the work: that of pairing the insects.

Unlike butterflies, moths will often mate in a very confined space, while most species can be paired in the well-known muslin meat-safes. These are circular, about 18 inches in diameter and 3 feet or so in length when open. The muslin is stretched over three cane hoops or wire rings. The upper part is conical and fitted with a hook from which the safe is hung when in use. There is a large opening at the bottom and this can be securely closed by a string which gathers the muslin together. A cage of this type has several advantages. It can be suspended where a current of air will pass through it, an essential for the successful pairing of many species; while, as insects often tend to fly upwards, the male and female are brought together in the conical top. Moreover, it is cheap, light, and collapses into a small space for storing.

As explained in *Butterflies*, hand-pairing has been successfully used in some species and, in the Genetic Laboratories at Oxford, Dr. P. M. Sheppard has lately applied the method to several of the Papilionidae (Swallow-tail butterflies) with excellent results. I do not think that this technique has ever been employed in mating moths, and its possibilities in that direction should certainly be investigated.

SINGLE-FACTOR DIFFERENCES

The action of single genes in producing variation is illustrated here by means of a few characteristic examples only. These are chosen from a considerable mass of material because they demonstrate particularly clearly the type of inheritance involved or because their effects throw light upon the classification or biology of moths. I am omitting instances of polymorphism since these will be discussed subsequently, in Chapter 5. For the same reason, I am, with a few exceptions, excluding also the genes responsible for industrial and non-industrial melanism (see Chapter 13). Though a knowledge of the principles explained in *Butterflies* is presumed here, I am giving instances which will provide some revision of them and help to relate them more specifically to moths.

The fundamental ratio of genetics, that of 1: 2: 1, results from a mating between two heterozygotes when all three genotypes are visibly distinct. Since, however, the characters produced by one of the two allelomorphs have usually become fully dominant, it is a relatively uncommon one. Indeed I was not able to illustrate it from butterflies, and had recourse to an example chosen from moths: the normal white form of the Currant Moth, *Abraxas grossulariata* L., Selidosemidae (Plate 11, figure 6), and its yellow variety *lutea* (figure 10). These are respectively the common and the rare homozygotes, and the heterozygote between them is of an intermediate pale yellow shade (figure 8). This therefore is not true-breeding but, on intercrossing, gives rise to normals, pale yellows and yellows in the proportion of 1: 2: 1. For these are the proportions obtained when two objects having alternative phases in equality, in this instance heterozygous allelomorphs, are combined at random. The statement remains true if we assort not genes but coins, two of which when tossed together fall both obverse, one obverse and one reverse, and both reverse in a 1: 2: 1 ratio. If the pale yellow form be crossed with either homozygote, equal numbers of heterozygotes (pale yellows) and homozygotes (normals or yellows) will appear among the offspring. This is the example actually discussed in the previous volume of this work, but now that we are dealing with moths several others could be cited. It will suffice to mention the Buff Ermine, *Spilosoma lutea* Hufn., Arctiidae (Plate 8, figure 5), and its blackish variety, known as *zatima*, the extreme forms of which are homozygotes (figure 7) and the less extreme heterozygotes (figures 8 and 9). Also the Scarlet Tiger, *Panaxia dominula* L., Hypsidae (Plate 11, figure 1 and Plate 14, figure 1), and its rare and striking variety *bimacula* (Plate 11, figure 2). The heterozygotes between these two are intermediates, though nearer to the normal form. They have been named *medionigra* (figures 3-5).

These three instances have been chosen in order to display different degrees of intermediacy between the heterozygote and homozygote. In the Currant Moth, the colour of the heterozygote is on the average about midway between that of the normal and the yellow forms; in the Buff Ermine and the Scarlet Tiger it respectively resembles more closely the rare and the common homozygote. Another feature of interest and importance is also demonstrated by these examples: in all of them the heterozygotes are the most variable while the normal homozygotes are the least so; a statement which can be regarded as having a wide application, as indeed is to be expected. For the normal form is likely to be so adjusted that its genes give the most favourable, and therefore constant, effects in the ordinary environment of the species. But organisms have insufficient opportunity to modify their reaction to rare varieties; and of these the heterozygotes poised, as it were, between two reactions, are likely to be less stable than the homozygotes.

Many rare varieties are complete recessives: that is to say, they are distinguishable only in the homozygous phase, the heterozygotes being apparently, or ' phenotypically,' normal and inseparable by inspection from the common homozygote. Consequently when such a variety is crossed with a homozygous normal individual, all the offspring, of the first or F_1 generation, will be normal also. If these are interbred the allelomorphs concerned segregate in a 1 : 2 : 1 ratio in the F_1 generation so produced. This therefore will consist of normal individuals and varieties in a ratio of 3 : 1 for, since the heterozygotes and normal homozygotes are indistinguishable, the first two terms of the 1 : 2 : 1 ratio are combined. The yellow form of the Garden Tiger *Arctia caja* L. (Plate 9, figure 6) is recessive to the ordinary one (figure 5), and so is that with the hind-wings streaked red and yellow (figure 7).

It will be remembered that on ' back-crossing ' a recessive, such as the yellow Garden Tiger, to the apparently normal heterozygotes, the succeeding generation will consist of (heterozygous) normals and varieties in equality. Such segregation, though also taking place, cannot of course be distinguished if the back-cross be made in the other direction: between the heterozygotes and red-winged homozygotes, since the two look alike.

In this instance the males and females, though of course differing structurally in many respects, have the same colour-pattern. There is, however, a marked difference between the sexes of the Common Heath, *Ematurga atomaria* L. Selidosemidae (Plate 9, figure 1 male and 2 female), and the beautiful recessive variety illustrated in figures 3 (the male) and 4 (the female) also has a different ground-colour in the two sexes.

Rare varieties are nearly always less hardy or less fertile than the normal form. That is one reason why the gene concerned does not displace its allelomorph and spread through the species. Indeed as will be explained in Chapter 13, certain black or ' melanic ' forms of moths represent almost the only known instance in which a rare variety is hardier than the typical condition, and this statement applies not only to the Lepidoptera, but to all living creatures, animals and plants. The fact that the genes so generally influence health and fertility indicates that they must have multiple effects and control the physiological processes of the body in addition to the simpler and more obvious characters of colour-pattern or the like, by which we are usually forced to judge their presence. Yet these may be much less important than variations in the vigour and reproductive capacity of the individual. A striking instance of this is provided by the Hebrew Character, *Orthosia gothica* L., Caradrinidae, (Plate 9, figure 8) and its recessive variety known as *circumsignata* (figure 9). This differs in the shape of the black markings in the centre of the fore-wings but, in addition it is completely sterile. Consequently it can only be produced from a mating between two heterozygotes, when of course one-quarter of the offspring will be of the sterile *circumsignata* form. It is not surprising therefore that it is exceedingly uncommon.

Genes may have the most diverse effects: they may influence colour, structure, habits, physiology or the genetic processes themselves, such as cross-over values or the mutation-rate. Thus on Plate 8 an example of interest to taxonomists* is illustrated. Figure 1 shows the normal form of the Scalloped Oak Moth, *Crocallis elinguaria* L., Selidosemidae, and figure 2 a recessive variety *brevipennis*. The gene concerned affects not only the pattern of the fore-wings, the central shade becoming narrower as it approaches the inner margin, but also their neuration, for the eighth nervure is suppressed. Now the neuration of the wings is one of the characters used in classification, and it is quite possible for a single hereditary factor so to alter such supposedly diagnostic features that the affected individual would be separated from its own species and placed in a different and sometimes very unrelated group, if judged on one of them alone. For example, Dr. D. Michie has studied a gene in mice which so modifies the urinogenital system as to provide the animal with a cloaca, a condition characteristic of the Monotremata, such as the Australian *Platypus*, but unknown in normal (Placental) mammals. I myself in examining great numbers of Swallow-tail butterflies have encountered exceptional specimens whose neuration is that of a distinct genus. The bearing of genetics on the evolution of geographical races will be discussed on pages 184-6, but it must be pointed out that in view of the profound and diverse effects of the genes it is essential to use as many distinct features as possible when assigning an insect to its systematic position. Decisions based upon the structure of the genitalia, or the neuration, alone are quite worthless. Furthermore, in most instances no indication is given of the number of individuals that have been studied in order to determine, for example, the anatomy of the normal genital armature of a butterfly or moth. Usually the illustrations are based upon the examination of very few specimens so that an entirely false idea prevails of the constancy of these organs. It is unfortunate that even in recent years an attempt has been made to discuss the basis of classification without taking proper account of the facts of genetics or the requirements of statistics, as has been done by Warren (1947).

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*Students of classification and nomenclature.

The varieties so far mentioned have intermediate heterozygotes or are recessives. Many, on the other hand, are dominants, like the black variety of the Willow Beauty, *Cleora rhomboidaria* Schiff., Selidosemidae, illustrated on Plate XXIV, figure 9; figure 8 is a typical example. When females of these are found in the wild, they will usually have mated with a normal specimen. Consequently the variety and the ordinary form will generally appear in equality among their offspring; in contrast with the result obtained by breeding from a recessive when fertilised in nature (*Butterflies*, pages 199-202). It sometimes happens, however, that a heterozygous dominant will mate with an individual of its own brood emerging in close proximity. In such circumstances a pairing between two heterozygotes may be secured, when three-quarters of the next generation will be varieties.

Any condition is sometimes called dominant if the gene responsible for it exercises a detectable effect when heterozygous. This is a mistake. A form is dominant only when the heterozygote is similar to one of the homozygous classes; it is important to adhere to this definition since complete dominance is the result of selection (page 214). Varieties of moths have frequently been listed as dominants when their homozygous form has never even been seen. In such circumstances there is no ground for knowing that this is identical with the heterozygote, or indeed that it exists; for the homozygous condition of rare varieties is frequently weak or sterile and sometimes lethal. In such circumstances a 2: 1 ratio, or an approach to it, is obtained when a 3: 1 ratio is expected. An example is provided by the dark variety of the Oak Beauty, *Biston strataria* Hufn., Selidosemidae, illustrated on Plate 8, figure 4, which is always a heterozygote, for the homozygous mutants die before reaching the imago state; figure 3 is the typical form.

From the account of gene-distribution given in *Butterflies* (pages 215-217), it will be remembered that in a wild population breeding at random the proportion of heterozygotes equals twice the product of the square roots of the two homozygous classes. Thus if the frequencies of the latter are respectively p^2 and q^2, the three genotypes are distributed in the ratio $p^2: 2pq: q^2$. Accordingly, if the heterozygous variety is uncommon, its homozygous phase will, even if fully viable, be very rare indeed and probably no entomologist will ever have seen it in the field. Thus in genetic work a form may only be described as dominant when the heterozygotes have been compared with both homozygous classes and found identical with one of them.

Information on the genetics of larval characters is badly needed at the present time. The subject is one on which anyone who breeds moths could contribute facts of importance, and here is an excellent field for amateur research. The complex colour-patterns and shapes of larvae are certainly variable: but that variation is largely undescribed and the mechanism of its control unknown.

The genetics of dark or blackish larvae have been studied in a few instances, but this will be considered in the section on Melanism (Chapter 13). An abnormality both of Privet Hawk and Poplar Hawk larvae, *Sphinx ligustri* L., and *Laothoe populi* L., Sphingidae, in which the segment bearing the posterior horn is duplicated, is known to be unifactorial and recessive. The normal form of the Privet Hawk is shown on Plate 21 and the two-horned condition on Plate XI. Dr. P. M. Sheppard has demonstrated a gene, recessive in effect, which influences larval colouring in the Scarlet Tiger (Plate XI) by changing the pale markings from yellow to white.

The larva of the Scarce Chocolate-tip, *Clostera anachoreta* Schiff., Notodontidae, has a white spot on the first abdominal segment. A non-spotted variety exists and this is a simple recessive. So too is a pale variety of the larva of the Currant Moth, illustrated in its normal form on Plate VI. On the other hand, Cockayne has shown that the absence of the yellow spiracular stripe in the larva of the Lesser

Swallow Prominent, *Pheosia gnoma* F., Notodontidae, appears to be a simple dominant.

Other genes affecting larvae are recorded but their number is small. One important generalisation can, however, be made in regard to them. That is to say, the genetics of the larval and imaginal stages are nearly always independent, even when the same type of variation is concerned. Thus melanic varieties are known in both the larva and the imago of the Early Thorn, *Selenia bilunaria* Esp., Selidosemidae (page 194), and they are unifactorial and recessive in both stages. Yet they are due to distinct genes: the black larvae give rise to typical moths and the black moths have normal larvae.

This generalisation follows from the fact that in the Lepidoptera the ecology of larva and imago is entirely different; indeed their whole mode of life and adjustment to their environment could hardly be more dissimilar. Thus it would be disastrous if the variation of the two phases were associated. It must necessarily be controlled by different sets of genes, in the same way that those responsible for the complete set of male and female characteristics are inoperative, or adjusted in a distinct manner, in the opposite sex. At any rate, a gene which modifies both larval and imaginal characteristics is likely to be subject to severe elimination by selection and consequently to be rare: so much so, that instances of the kind are very difficult to quote, but the North American butterfly *Colias philodice* Godt., supplies one. The egg, larva, pupa, and eye of the imago are all coloured by a yellowish-green pigment, related to chlorophyll, which is changed to blue by a gene recessive in effect. It has been shown that the condition destroys the cryptic adjustment of the larvae, for in segregating families exposed to the attacks of birds the mutants are eaten while the normal specimens escape.

Multiple Allelomorphs and Linkage

It is disappointing to find that multiple allelomorphs have not so far been established with certainty in any of the larger British moths,* though in several species a graded series of forms, some or all of which are known to be unifactorial, is strongly suggestive of them: for instance the red, salmon-pink and yellow varieties of the Six-spot

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*The ground-colour of the wings is controlled by a series of multiple allelomorphs in the Tortricid *Peronea comariana* Zell. They have been studied also in *Ephestia*.

Burnet, *Zygaena filipendulae* L. (Plate 8), and the red, striated and yellow ones of the Garden Tiger (Plate 9). Their analysis should rank as a high priority on the list of genetic investigations to be carried out in the Lepidoptera. There can be no doubt that in this field, as in linkage (pages 29-33), the failure of entomologists to study the simultaneous segregation of two pairs of allelomorphs has retarded the advance of knowledge.

The significance of multiple allelomorphism and the means for detecting it are described in *Butterflies* (pages 188-191). It can here usefully be illustrated by the Garden Tiger varieties to which reference has just been made. Both the yellow form and that with the hind-wings striated red and yellow are simple recessives. Suppose their genes are multiple allelomorphs. We then have the situation that the yellow $=$ yy, the striated $= y^s y^s$, while the normal red $=$ YY. The heterozygotes Yy and Yy^s are also red. On mating the yellow and striated forms, the combination yy^s only will be produced. This, on analogy with multiple allelomorphs in general, will be intermediate between the two mutants, presumably yellow with a trace of red striations. On intercrossing, however, this type will give rise to yellow, slightly striated and fully striated in a 1 : 2 : 1 ratio.

Consider, alternatively, what would happen if these genes were at different loci. Each would then carry the normal allelomorph of the other. The yellow would therefore have the constitution yySS and the striated YYss. On mating yellow and striated insects, all the offspring would be *normal red* specimens of the constitution YySs. These on intercrossing would produce normals, yellows, striated forms, and a form combining the two recessive characters, in the ratio of 9: 3: 3: 1. The two situations, those in which the genes are multiple allelomorphs and in which they occupy separate loci, are clearly distinguished by these sets of results.

A few instances of multiple allelomorphs have in fact been established in moths, though not in the larger British species. However, an additional example is provided by *Aglaia tau* L., a European member of the Saturniidae. Here the two mutant genes are both semi-dominants. This is a large brown insect with an eye-spot in the centre of each wing. However, in the variety *melaina* the male is black and the female blackish brown above, but with pale undersides. A second variety, *fere-nigra*, is blackish with a yellow median area above, but it is darker than *melaina* below. These are each unifactorial, and since

Plate 3. MIGRANT AND NEWLY DISCOVERED SPECIES

1
S. DEVON

2
SALISBURY

3
OXFORD

4
CRUMBLES,
SUSSEX

5
FOLKESTONE

6
READING

7
PEMBROKE

8
WALMER,
KENT

9
HAMPSHIRE

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1. White-L Wainscot, *Leucania l-album;* 2. Brighton Wainscot, *Oria musculosa;* 3. Humming-bird Hawk, *Macroglossa stellatarum;* 4. Vestal, *Rhodometra sacraria;* 5. Rest Harrow, *Aplasta ononaria;* 6. Striped Hawk, *Celerio livornica;* 7. Ni Moth, *Plusia ni;* 8. American Wainscot, *Leucania unipuncta;* 9. Crimson Speckled, *Utetheisa pulchella*

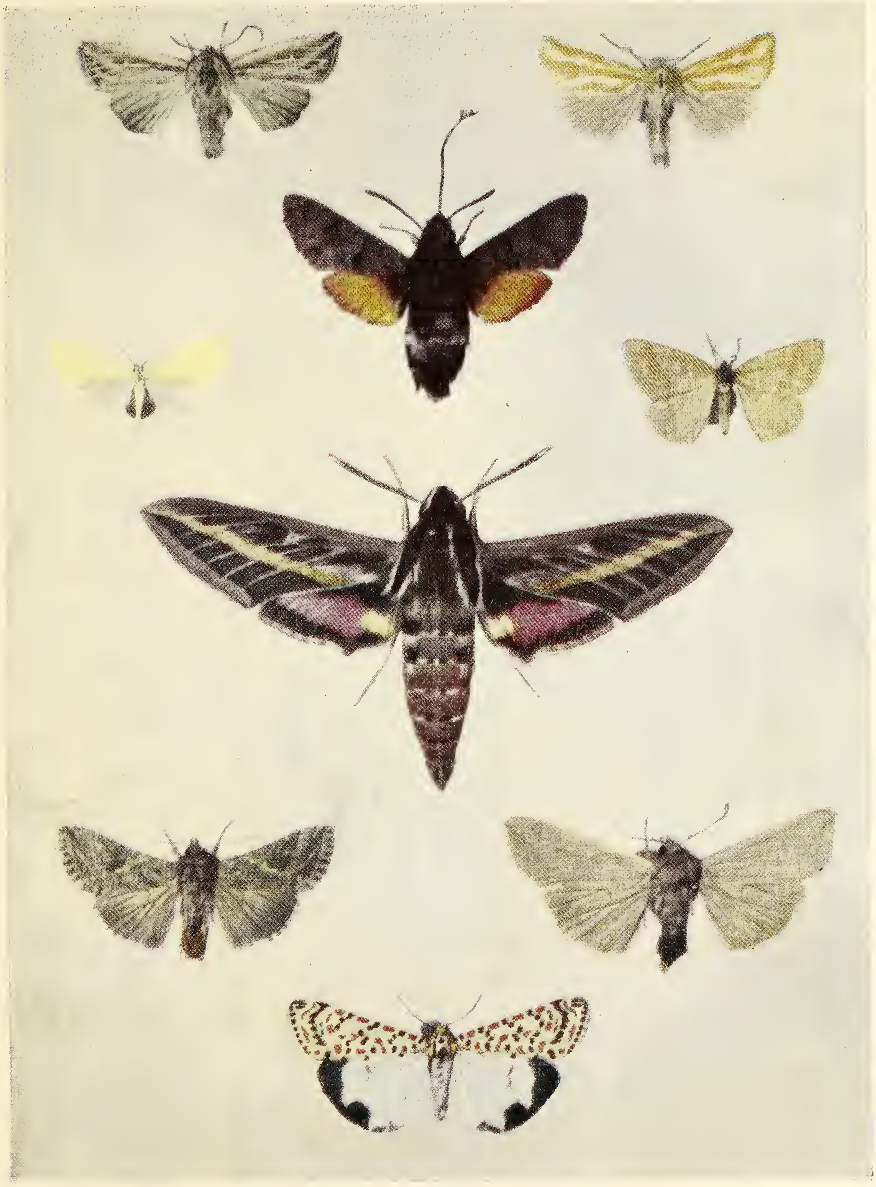
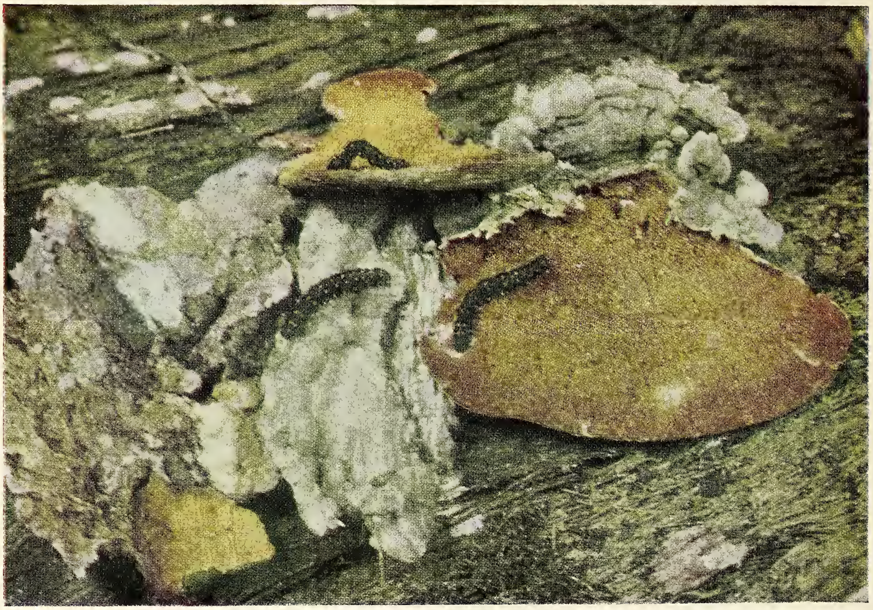


Plate 3



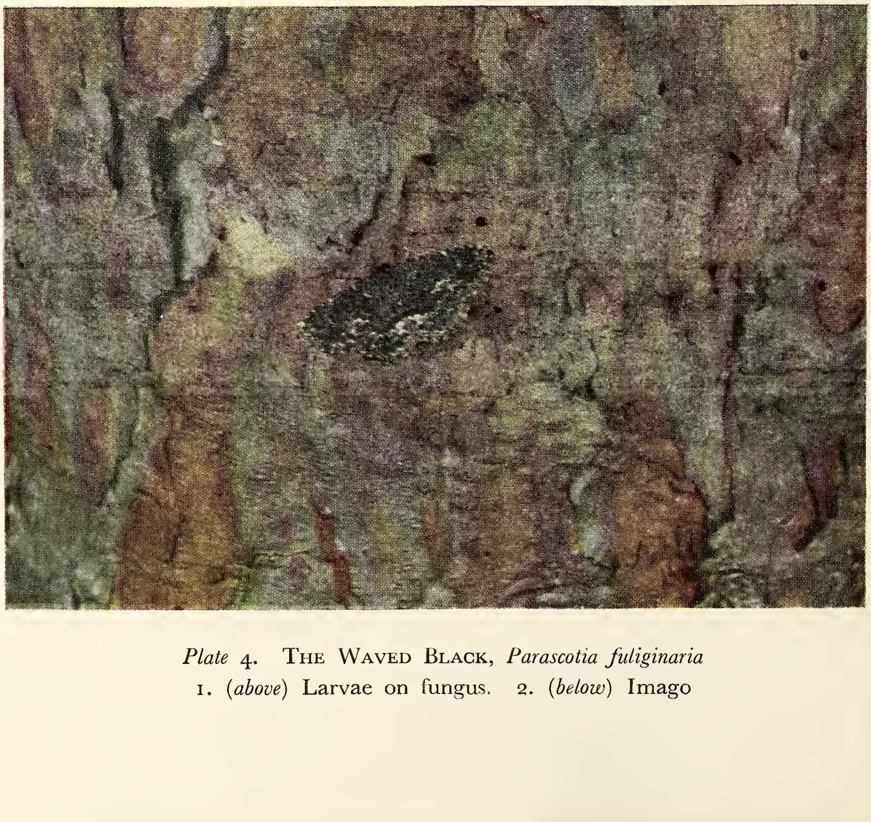


Plate 4. The Waved Black, *Parascotia fuliginaria*
1. (*above*) Larvae on fungus. 2. (*below*) Imago

their genes are multiple allelomorphs they can be combined only as a single dose of each, producing a form which has been called *weismanni* which unites the characteristics of the two varieties. Genetically, there fore, the situation may be represented thus: *tau*=mm; *melaina*=Mm and extreme *melaina*=MM; *fere-nigra*=M^{F}m and extreme *fere-nigra*=M^{F}M^{F}, while *weismanni*=MM^{F}. Consequently when two specimens of *weismanni* are crossed, they give rise to *melaina*, *weismanni*, and *fere-nigra* in a ratio of 1: 2: 1.

The simultaneous segregation of two pairs of allelomorphs, each with complete dominance, results in a 9: 3: 3:1 ratio in the F_2 generation, and in the production of four classes in equality when a double heterozygote is back-crossed to a double recessive, provided that two assumptions be made: that the different classes are equally viable, and that the genes controlling them are carried in different pairs of chromosomes and consequently assort independently of one another. These facts have been explained in *Butterflies* (pages 181-185). So too (pages 185-188) has the exception to them consequent upon the carriage of two pairs of allelomorphs in the same pair of chromosomes. This results in *linkage*, a phenomenon which requires slightly fuller treatment here than was accorded to it in the previous volume.

The literature dealing with genetic linkage is vast, and its detailed analysis necessitates appropriate statistical treatment (Fisher 1950; Mather 1946, 1951). Autosomal linkage has been reported in the British 'Micro-Lepidoptera' in one or two instances,* but it is disappointing to find that it has not yet been analysed in detail in any of the species which are the subject of this book. There are two reasons for this. First, the large number of chromosomes in the Lepidoptera, amounting usually to several dozen pairs, is not favourable to the discovery of linked genes. Secondly, as already pointed out, entomologists have so seldom studied the simultaneous segregation of two pairs of allelomorphs.

It is clearly desirable to establish the linkage relationships of the genes investigated in the Lepidoptera but, as indicated on page 19, the group is not well suited to work on the physical basis of heredity, and it is better to concentrate on exploiting its exceptional value as

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*In *Peronea comariana* Zell., Tortricidae, there is close linkage between the gene controlling the colour of the costal blotch (black, dominant; brown, recessive) and the series of multiple allelomorphs responsible for the ground-colour of the forewings.

material for the study of evolution and physiological genetics. However, following the account already given in *Butterflies*, some additional information on the significance of linkage may be welcome, while the means for detecting it can appropriately be restated more fully with reference to an example drawn from moths.

A great many varieties of the Garden Tiger are known. In one of them, *petriburgensis*, the dark marks, both the chocolate on the fore-wings and the black on the hind-wings, are reduced in size.* This behaves as a simple recessive to the ordinary pattern while, as already indicated, yellow hind-wings are recessive to the normal red.

If a typical Garden Tiger heterozygous for these two genes be crossed with yellow *petriburgensis* the possible combinations of these characters (red and yellow with normal pattern, red and yellow *petriburgensis*) will of course segregate in equality among the offspring, provided that the genes are carried on different chromosomes as, in fact, they probably are. Following the accepted nomenclature, they may be distinguished as P=normal pattern (*caja*) and p=*petriburgensis*, Y=red hind wings, y=yellow.

Suppose, on the other hand, these genes are linked. Those carried in the same chromosome are written on the same side of a line. Thus the doubly heterozygous insects may be PY/py and the double recessives py/py. In these circumstances, P and Y travel in the same vehicle and generally therefore reach the same destination; that is to say, the same gamete. So do p and y. Thus on crossing the heterozygous normals with yellow *petriburgensis*, the two parental types resulting from the gene combinations PY/py (PY derived from one parent and py from the other) and py/py will be the most frequent and will appear in equality. But blocks of material are interchanged between the pairs of homologous chromosomes during the formation of the gamete, and if one of the points of transference occurs between the positions occupied by P (or p) and Y (or y), P will of course be included with y and p with Y. This will produce the types Py/py (P and y coming from the heterozygous parent and p and y from the double recessive) and pY/py (p and Y from the heterozygote and p and y from the double recessive), so giving rise to a few yellow normals and red *petriburgensis* in equality.

Linkage therefore will result in an excess of the original two classes

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*The characteristic feature of this variety is the absence of band F (the sixth from the base) on both fore and hind wings.

(in equal numbers) and the production of a few of the two ‘ recombination classes,’ in equality also, due to the exchange of blocks of material between homologous chromosomes, known as *crossing-over*. If the allelomorphs concerned are situated far apart on the chromosomes (thus P————————————Y) a cross-over will often occur between them and separate them. If, on the other hand, they are near together (thus PY————————————) the chance of an interchange taking place in so short a length is small. The presence or absence of linkage therefore demonstrates whether any two genes are situated in different chromosomes or in the same one; while, in the latter event, the frequency of crossing-over between them is an indication of their distance apart. This is measured by the cross-over value (C.O.V.) which is calculated as the percentage of the two re-combination classes added together.

Thus in the example just given, if 25 per cent of the offspring belong to each of the four possible classes, the genes controlling them are carried in different pairs of chromosomes. Suppose, on the other hand, that the back-cross family consists of 49 per cent of normal *caja*, 49 per cent yellow *petriburgensis*, 1 per cent yellow *caja* and 1 per cent red *petreburgensis*. This is evidence of close linkage between the two genes concerned, and their C.O.V. = 2.

It has been stated that linkage reduces the frequency of the ‘ recombination classes.’ But which are they? In the present instance the two dominant genes are carried in one chromosome of the heterozygote and the two recessives in the other (the so-called ‘ coupling ’ phase). They might have been differently arranged, with one dominant and one recessive in each (Py/pY). This is the so-called ‘ repulsion ’ phase. It would still produce an individual of normal appearance but, when crossed with the double recessive, it would now be P and y, p and Y which would hold together, giving an excess of what were before the two rarer classes. This would be of the same magnitude (in the example chosen, 49 per cent instead of the expected 25 per cent of each) since that depends on the distance apart of the genes, not on their arrangement. The back-cross family would now consist of 1 per cent normal *caja* and 1 per cent of yellow *petriburgensis*, 49 per cent yellow *caja* and 49 per cent red *petriburgensis*. Thus though the parents look the same the recombination classes are different, though their C.O.V. is still 2.

Not unless we know the parents of the double heterozygote is it possible to state in advance whether P is in the same individual chromosome as y or Y. For if these are red *caja* and yellow *petriburgensis* the coupling phase would be produced, while if they are yellow *caja* and red *petriburgensis* the double heterozygotes will be in repulsion. Thus the full analysis of crossing-over requires the study of three generations.

We here reach an important conclusion frequently missed in the elementary discussion of genetics. Since mutation and crossing-over (between any two loci) are recurrent phenomena, the latter being on the average immensely more frequent, the coupling and repulsion phases will be equally common in the total population. Thus on the average any two linked genes will be kept apart as often as they are associated. Consequently linkage is not a mechanism capable of ensuring that two qualities shall generally be inherited together in the species as a whole, though it may be so within particular families. For instance, Cockayne has indicated a probable instance of close linkage in the Oak Eggar, *Lasiocampa quercus* L. The variety *olivaceofasciata* is dark with a greenish, instead of a tawny, band on the forewings, and it is probably a simple recessive; so too is the blackish form of the larva. These larval and imaginal conditions were formerly thought to be effects of the same gene. It is now known, however, that though in some localities dark larvae always produce dark moths while normal larvae never do so, in other places the two conditions are independent. This is precisely the situation to be expected with very close linkage. Were the genes further apart on the chromosomes, families in which the two recessives tend to remain together would everywhere be balanced by those in which they tend to be separate. If two distinct hereditary qualities are constantly associated (like mental deficiency and the presence of phenyl-pyruvic acid in the urine, as in the disease phenylketonuria in Man), the most probable interpretation is that they are distinct effects of the same gene.

Linkage of course leads to departures from the dihybrid ratio, just as it does from the back-cross type of segregation. That is to say, coupling produces an excess of the two end-terms of what should be a 9: 3: 3: 1 ratio and repulsion an excess of the two middle ones.*

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*It should be noticed, however, that for statistical reasons the dihybrid ratio provides a sound method of estimating the cross-over value only with close linkage in the coupling phase; with loose linkage in coupling, and in all instances of repulsion, back-cross segregation must be used.

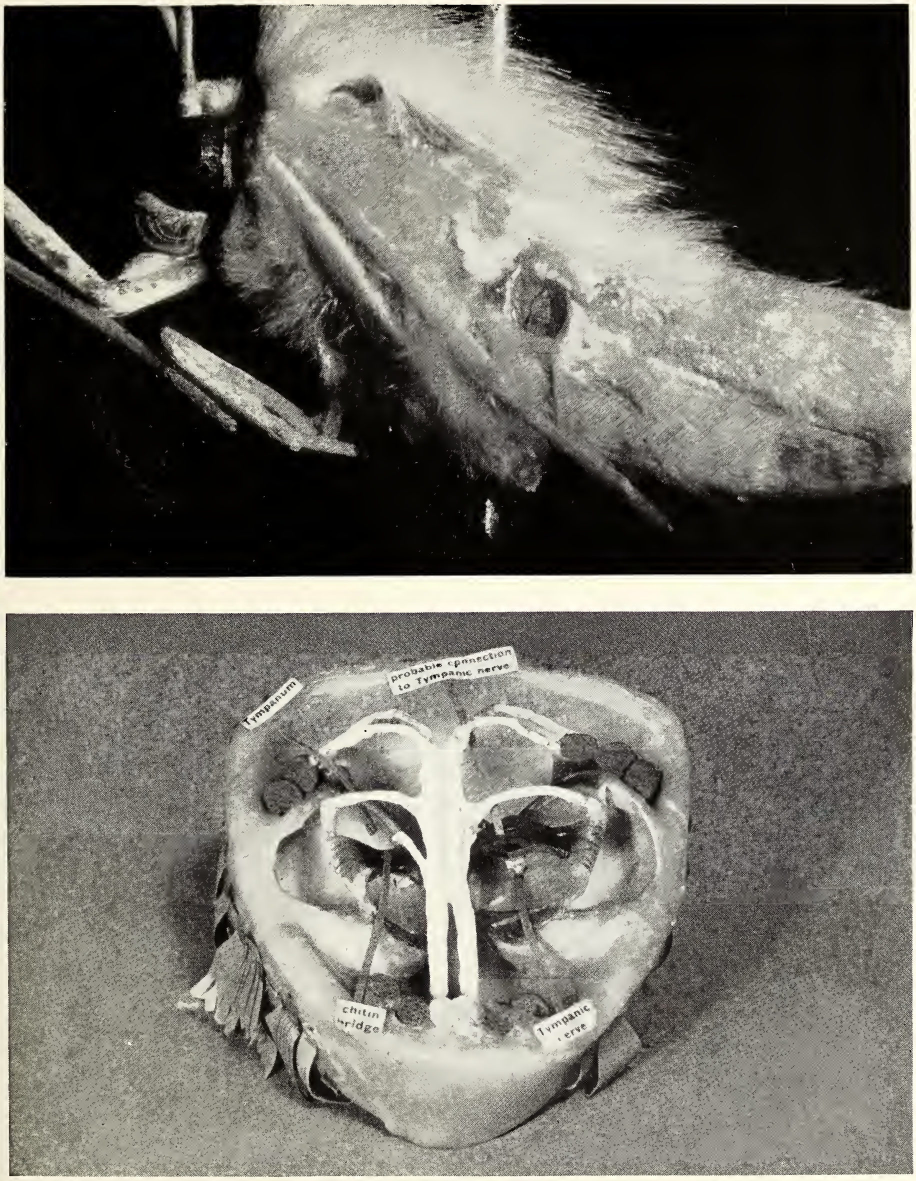
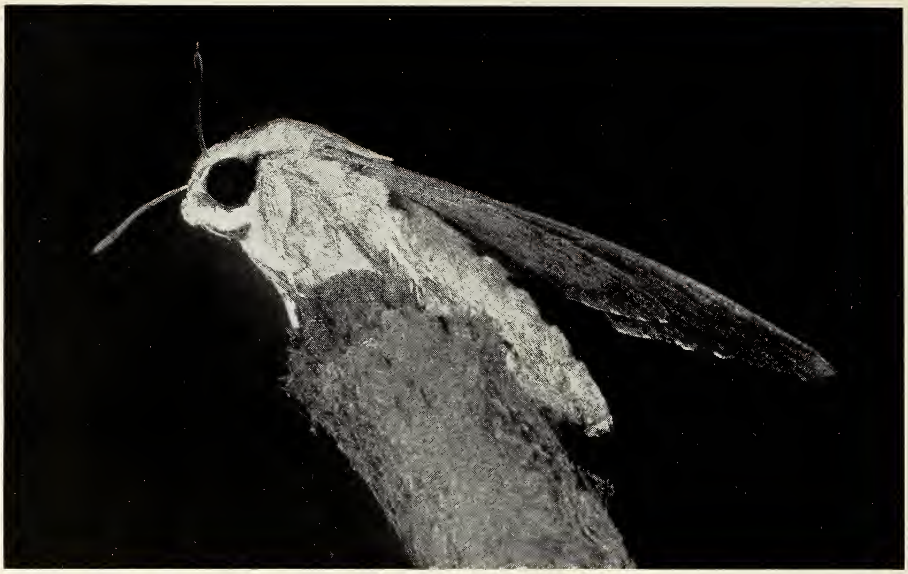

Tympanum
probable connection to Tympanic nerve
chitin bridge
Tympanic nerve

Plate I. THE EARS OF MOTHS

1 (*above*). Swallow-tailed Moth, *Ourapteryx sambucaria*, showing ear (X 8); 2 (*below*). Model of a Moth's Ear, seen in transverse section of body



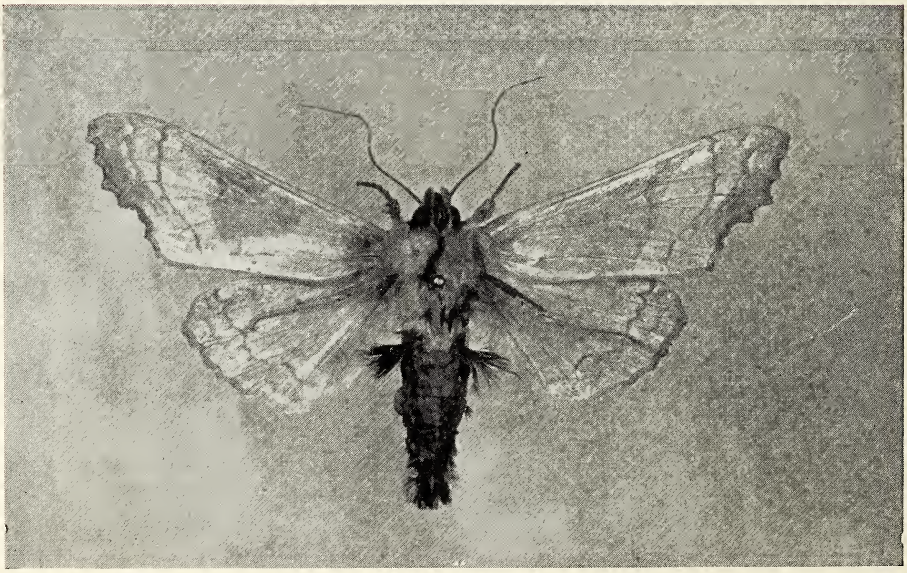


Plate II. THE EYE AND SCENT BRUSHES

1 (*above*). Convolvulus Hawk, *Herse convolvuli* showing Eye (X 1.5); 2 (*below*). Angle-Shades, *Phlogophora meticulosa* showing abdominal scent-brushes (X 2)

An excess of any other terms (for instance the two last) or of a non-recombination and of a recombination class of a 1:1:1:1 ratio is usually the result of the unequal viability of the types: at any rate it does not indicate linkage.

These facts should make it possible to detect linkage in the Lepidoptera, and to study it at an elementary level. If discovered, a fuller account of the subject should be consulted, as the situation is over-simplified here: for instance, large cross-over values may give the effect of independent assortment, and very close linkage that of allelomorphism. Moreover, proper statistical treatment is essential in this field of genetics (see Fisher, also Mather *l.c.*).

MUTATION

Mutation is a change in any unit of heredity (a gene or a chromosome), and has been briefly described in *Butterflies*, pages 197-8, to which reference should be made. The genes are extremely large molecules and therefore they are to some extent unstable compounds in the chemist's sense. Consequently they are subject to intrinsic changes, or mutations; but these occur at a very low frequency: the average value at a locus is probably less than one in a million per gamete. However, there is much variation in this respect, and mutation-rates twenty times greater than this are known, but they then approach their upper limit. It should be added that the recent work of Buzzati-Traverso suggests that natural mutation-rates may be somewhat greater than has previously been suspected, and that the variation they supply is checked by a greater degree of selection. Even so, they are very rare, and the significance of this has already been considered in *Butterflies*, (*l.c.* and page 277).

Mutations are not confined to the reproductive cells but can occur also in those of the body. If taking place at an early stage in development, they may give rise to abnormal patches of tissue. Three of the extraordinary conditions illustrated on Plate 12 may be of this kind: figure 1, the Garden Tiger, with a sector of the fore-wing pattern on the left hind-wing; figure 2, a larva of the Cinnabar Moth, *Hypocrita jacobaeae* L., Arctiidae, exhibiting spiral segmentation (though this is also known as a result of genetic segregation in other organisms): and the Six-spot Burnet Moth, figure 5, in which a hind-wing replaces a fore-wing on the right side.

I wish here to draw attention to one aspect of genetics which has been explored in detail in many organisms, animal and plant, but strangely enough very little in the Lepidoptera. This is the artificial induction of mutation by chemical and physical means. Certain chemicals, such as colchicine and mustard gas, can give rise to mutations (principally of the chromosomal type, owing to their influence upon cell-division); but a method of far more general application is provided by penetrating radiation, which is powerful also in producing changes in the genes.

All kinds of short-wave radiation are capable of inducing mutation: X-rays of varying lengths, β-rays of radium, the γ-rays of radio-active substances, and neutrons, and they all do so to an equal degree as judged by ionization-rate. Their action is additive in time, so that separate small doses given at intervals are equivalent to a single large one of corresponding amount. Moreover, the effect is a direct linear one; that is to say, a doubling of the dosage produces twice as many mutations. Consequently it can be extrapolated in either direction, to answer the question whether normally occurring spontaneous mutation is due to the minute amount of short-wave radiation to which organisms are naturally exposed, both from surrounding objects and as cosmic rays from other worlds. It is, in fact, found that, rare as are spontaneous mutations, they seem to be about a thousand times too frequent to be due to this cause. To put it another way, about one in a thousand of them is actually induced by the short-wave radiation occurring naturally. The rest flows from the fact, already mentioned, that the genes are of course not completely stable compounds.

It is possible, in moths as in other organisms, to produce mutant genes in large numbers by irradiation, and consequently to increase greatly the genetic variability of stocks of Lepidoptera among which varieties, striking or otherwise, would begin to segregate. The reasons for doing so are not so cogent as in some other types of material better suited to analysing the mechanism of heredity (page 19). For work of that kind large numbers of mutant genes are invaluable. But from the experimental point of view the special advantage of the Lepidoptera is their suitability for the investigation of evolutionary genetics, and mutation does not control evolution. It is true that these insects provide material of great value for studying gene-action, and for that purpose it would be highly desirable to augment the number of available mutants. These would also supply moth-collectors with new aberrations to add to the series in their cabinets; but that is indeed a poor reason for undertaking the artificial induction of mutation.

When, as it certainly will be, penetrating radiation is more generally used to induce mutation in the Lepidoptera, we may hope that the variation so liberated will escape the attention of the more formal students of nomenclature. The names of animals and plants are mere handles for the use of scientists and naturalists, not a serious study nor an end in themselves. International Rules of Nomenclature are indeed salutary so long as they are our servants not our masters. When the name of an organism has become widely accepted it should not be changed on account of priority, but should be fixed by an International Committee in spite of others which ante-date it; as is occasionally done already, though much too seldom. A system of naming genes, and the varieties to which they give rise, without reference to the International Code as applied in taxonomy, has proved entirely satisfactory in the field of genetics, including the complex one of the *Drosophila* literature: International Rules as used by taxonomists should not be allowed to impinge upon it.

We are told that we are entering an Atomic Age, and accordingly we are asked what will be its effects upon animals and plants. The answer is, upon their variation exceedingly little and upon their evolution none: this of course apart from their actual destruction by atomic explosions. The great majority of mutations are disadvantageous, for their occurrence is at random relative to the needs of the organism and one cannot make random changes in a highly complex system, such as the body of an animal, and expect to promote its harmonious working. Occasional advantageous mutations certainly do arise, perhaps a little more often than has been thought in the past, but evolution is controlled by selection acting upon the genetic variability supplied by recombination and genic interaction.* Fortunately it is not determined by the frequency or kind of mutation which occurs. Moreover, it is difficult to conceive the use of atomic energy at dosages that can do more than increase slightly the mutant genes of organisms and therefore the burden of maladjustment which must the more rigorously be removed by selection.

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*The diversity of the allelomorphs upon which this depends has indeed been produced by mutation in former generations; but this provides only potential variability on which selection can operate, so that its nature does not control the evolutionary processes.

CHAPTER 3

THE GENETICS OF SEX

Sex-determination

The account of sex-determination and the phenomena associated with it given in this chapter extends that already outlined in *Butterflies* (pages 191-197). It will be recalled that in the Lepidoptera, as in most higher animals, the sex-determining agents are the *sex-chromosomes*. In male moths these consist of a corresponding pair, the X-chromosomes. Females, however, possess but one of this type, whose partner, the Y-chromosome, is in some respects abnormal, carrying relatively few genes. The number of X-chromosomes, one or two, not the presence or absence of Y, is the deciding feature in sex-determination. If an additional Y-chromosome is by accident included in a cell its effect is negligible, but additional X-chromosomes profoundly influence the sex of their possessor. The simple distribution of the X- and Y-chromosomes to produce males and females in approximate equality is shown diagrammatically on page 192 in *Butterflies*.

Individuals with similar (XX) and dissimilar (XY) sex-chromosomes constitute respectively the *homogametic* and *heterogametic* sex. The latter is usually the male; it is the female only in the Lepidoptera and a few other groups, which include the nearly related Trichoptera (caddis-flies), the birds and some fish. Thus in moths it is the female but in mammals, and therefore in man, the male who decides the sex of the offspring.

The mechanism of sex-determination must now be considered in somewhat more detail. It is vested not in the whole of the sex-chromosomes but in one part of them, their differential segments, which in X and Y remain permanently distinct, for no crossing-over takes place between them. However, since the differential segments of the two X-chromosomes correspond to one another, they can undergo crossing-over in the homogametic sex. The other part of the sex-chromosomes, their 'pairing region,' consists of material which is similar in X and Y and can always therefore be interchanged between them (see Figure 2). That is to say, the distinction between the X- and Y-chromosomes is valid for their differential segments only.

Sex is determined by the action of many genes situated not only in the sex-chromosomes but in all the others, which are collectively known as *autosomes*. Some tend to promote male and some female development. Those of female tendency predominate in the autosomes and the pairing region of the sex-chromosomes, those of male tendency are chiefly localised in the differential segment of X but are absent from that of Y. The fixed dosage of the genes for femaleness, both in the autosomes and the pairing region of X and Y, is effective in competition against the single set of male determinants in one sex-chromosome but its action is overpowered by the double set carried in two. Consequently the XX condition produces maleness and the XY femaleness in the Lepidoptera. In the majority of animals, where the heterogametic and homogametic sexes are reversed, the differential region of X is of course predominantly female in effect and the rest of the chromosome material predominantly male.

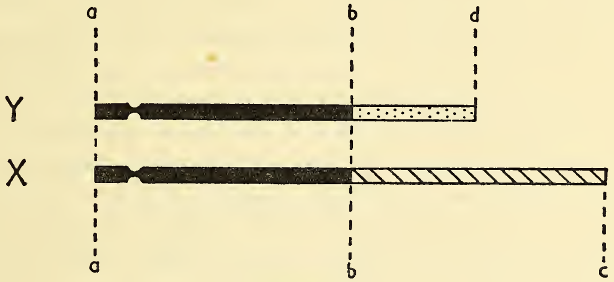


FIGURE 2

The sex-chromosomes, X and Y, may be of similar or different lengths, though here Y is represented as the shorter. Each possesses a section of corresponding material (a-b) and a differential segment (b-c in X, b-d in Y) which remains distinct. The constriction is the centromere

Sex-intergrades

Owing to an abnormal cell-division, an X-chromosome may be lost from one of the cells of the homogametic sex, so converting it and the cells derived from it to the heterogametic type, and therefore changing them from male to female. Similarly the two products of a chromosome-division may occasionally move to the same pole and be included in one daughter-cell, so giving rise to an XX condition in the heterogametic sex: the companion cell, being left without any X-chromosome, will die. Either of these events produces an individual in which some parts of the body are male and others female. For, as explained in *Butterflies*, the sex of the tissues is, in the Lepidoptera, that of the cells composing them; whereas in mammals it is controlled by the chromosomes at second-hand as it were, through the agency of hormones secreted by the sex-glands, the testes or ovaries.

Specimens of mixed sex due to an abnormal distribution of sex-chromosomes are known as *gynandromorphs*, and the male and female parts develop simultaneously in them. Should the first cell-division of the embryo be the abnormal one, one-half of the insect will be male and the other female, the line of demarcation falling rather accurately along the mid-line of the body. Two examples of this, both striking on account of the great sexual differences involved, are illustrated on Plate 12. Figure 7 shows a specimen of the Bordered White, *Bupalus piniarius* L., Selidosemidae, in which the left side is female and the right male; and figure 6 the Winter Moth, *Operophtera brumata* L., Hydriomenidae. In this latter species the male (here the left side) is fully winged, while the female (here the right) is nearly apterous.

When gynandromorphism appears later in development, the inappropriate sex occupies a small part of the body only, producing a patch of male tissue in a female or the reverse. It occasionally results also from the inclusion of two nuclei in one egg. These may each be fertilised and, if they carry X- and Y-chromosomes respectively, their subsequent division gives rise to cells of different sex and so to a moth which is partly male and partly female. Though gynandromorphism of this kind has been detected in the Lepidoptera, the phenomenon has been more extensively studied in other forms (especially *Drosophila*) and its origin from an abnormal cell-division is known to be far the commoner. This can also produce sexual abnormalities at any period of development, while the binucleate type can do so only in the early stages. The tendency to form gynandromorphs, by either means, is inherited and is often unifactorial.

Gynandromorphism resulting from a binucleate egg is, with fair probability, illustrated by two remarkable specimens on Plate 12. Figure 4 is a bilateral gynandromorph of the Waved Umber, *Hemerophila abruptaria* Thnbg., Selidosemidae, in which the right side is male and the left female. The difference in the antennae, simple in the female and brush-like in the male, is visible in the Plate, while the composite structure of the external genitalia can be seen when the specimen itself is examined. However, in this insect a colour-difference is also involved, the left side being normal and the right of a deep chocolate shade.

The known melanism of this species is autosomal, so that ordinary gynandromorphism through an incorrect distribution of the sex-chromosomes seems here to be excluded. But for a curious additional fact, another and rarer type of chromosome abnormality might account for it. That is to say, since the male-determining genes carried in the differential segment of the X-chromosome are balanced against others of female tendency carried in the autosomes, it is clear that the adjustment between the two will be affected by the loss of one of the autosomes. This is nearly always fatal when these are few and large; but where, as in moths, they are small and numerous, it is not necessarily so. In the fly *Drosophila melanogaster* we know that the sex-genes exist in large numbers and that they all have slight effects of about equal magnitude, but in the related *Drosophila simulans* some are much more important than others. Thus it might have been suggested that Figure 4 is a gynandromorph due to the loss of an autosome, one which carries both the gene for melanism and one or more female-determining genes of sufficient importance materially to influence the balance of sex.

The additional circumstance, apparently excluding that possibility, is the fact that the specimen illustrated was one of four gynandromorphs in the same brood. Three of these were melanic males on the right and normal females on the left side, while the fourth was a melanic female on the right and a normal male on the left. It seems probable therefore that these insects developed from eggs with two nuclei, one with an X- and the other with a Y-chromosome. The autosomal gene for melanism and its normal allelomorph could have segregated either in these or in the sperms which fertilised them.

The different colouring on the two sides of the Currant Moth, *Abraxas grossulariata* L., Selidosemidae, shown in figure 3 is much more easily interpreted, since pigmentation alone is involved. Sexually the specimen is a normal female. We are not therefore faced with the concurrence of two exceptional conditions. Somatic mutation is probably responsible for it. Alternatively it may be produced by a reverse mutation to the ordinary form; for some of the known genes producing melanism in this species are recessives, consequently the loss of an autosome may account for the situation; so also, but less probably, could development from a binucleate egg, the two fertilising sperms of the male parent supplying the segregating colour-genes. Since the specimen is a normal female, the two nuclei of the egg would both carry a Y-chromosome. This is the condition which would result if X had passed into the first polar body while the two daughter nuclei (each with Y), formed during the second meiosis, had remained together instead of segregating into the egg and another polar body.

The term " sex-intergrade " indicates an individual of mixed sex however produced. As we have just seen, it may arise as a result of gynandromorphism, which involves an error in the mechanical distribution of the sex-chromosomes. On the other hand, an *intersex* is a hermaphrodite due to a lack of balance between the sex-determining genes. Individuals of this type tend to appear among the offspring of a racial cross, usually involving different sub-species or species.

It has been pointed out that the genes for maleness and femaleness must be so balanced that, in the Lepidoptera, one set of the male determinants is in effective deficit and two sets are in effective excess compared with the fixed dosage of female determinants contributed by the autosomes and the pairing regions of X and Y. That is to say, it is their relative amounts which are important; provided that this relationship is maintained, their absolute values are immaterial and may be modified as selection, in the presence of isolation, builds up a different genetic constitution in different races.

This situation becomes clear if we arbitrarily assign numerical values to the quantities of sex-determinants supplied by the genes. In one race (A) the male type may contribute 40 units and the female 60: one is therefore always in excess of the other by 20 units (40: 60 or 60: 80). In another race (B) the values may be 80 units of male-

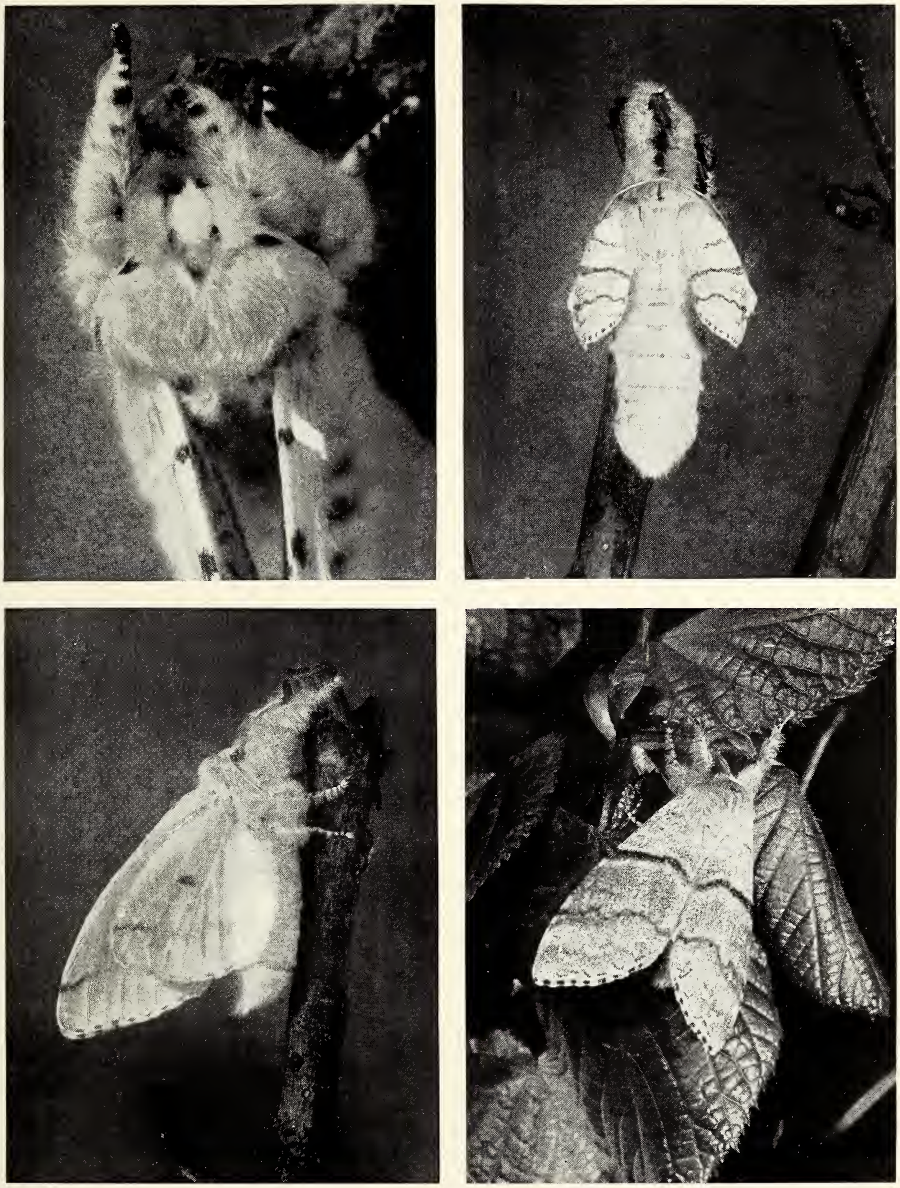


Plate III. The Frenulum and the Development of a Moth's Wings

1 (*top left*). Puss Moth, *Cerura vinula* showing male frenulum and retinaculum; 2-4 (*top right, and below*). The Pale Tussock, *Dasychira pudibunda*, the development of the wings (all X 1.5)

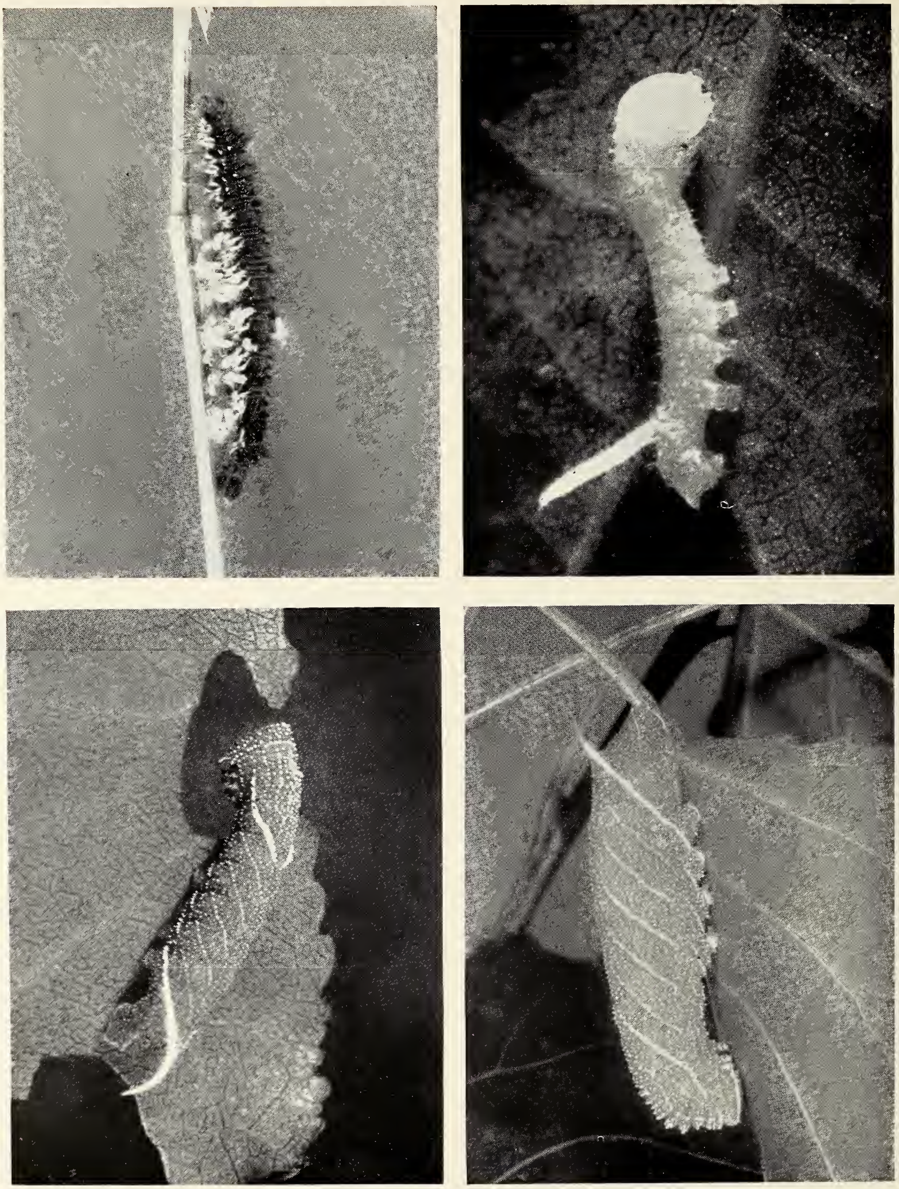


Plate IV. Parasitised Larva and the Relative Growth of a Larval Horn
1 (*top left*). Drinker Moth, *Philudoria potatoria*, larva and its parasites (X 1)
2-4. Poplar Hawk, *Laothoe populi;* 2 (*top right*), larva newly hatched (X 10); 3 (*lower left*), partly grown (X 2.5); 4 (*lower right*), fully grown (X 1)

determinants and 120 of female, so that one is still always in excess of the other, this time by 40 units (80: 120 or 120: 160). But on crossing individuals from two such distinct populations, one type may not exceed the other by the necessary amount. The hybrids will possess half the sum of the female components of each race; that is to say $\frac{1}{2}(60+120)=90$. This, balanced against the X-chromosome derived from race B which contributes 80 units of male-determinants, provides an excess of but 10 units. It is therefore only half that allowed even in the race with the smaller values, and may not be sufficient to ensure normal sexual development. If so, a sex-intergrade of the intersex form would result. Different amounts and combinations of the sex-determinants brought in by racial crossing can give rise to intersexes of varying degree, both in individuals with XX- (intersexual males) and with XY-chromosomes (intersexual females).

An intersex develops completely as one sex for a period of time and then changes and develops as the other. The earlier that this turning-point occurs, the more extreme will be the intersexuality. Thus the organs are affected in the reverse order of their development, those appearing the latest in embryology, such as the wings, being the ones influenced by a slight degree of intersexuality, while those that are laid down early, as are the testis and ovary, are among the last to be affected. It will be realised therefore that in gynandromorphism parts of different sex develop simultaneously in the body, while in intersexuality they develop one after the other; so that it has been said that gynandromorphs and intersexes are respectively sex-intergrades in space and in time.

If the turning-point of intersexuality occurs early enough, it will bring about a total sex-reversal: a conversion of potential males to normal females or the reverse. In this way the heterogametic and homogametic sexes could be interchanged, a result which has actually been achieved experimentally. The singular fact that the XY type is female in some groups and male in others becomes less mysterious in the light of such work. Indeed Winge (1932), using the fish *Lebistes*, has not only interchanged the sex-determining mechanism but, by selecting sex-genes of different potency, has converted sex-chromosomes into autosomes and autosomes into sex-chromosomes.

Intersexuality has been studied in great detail by Goldschmidt in the Gypsy Moth, *Lymantria dispar* L., a species in which the males are dark brown and the females whitish (Plate 32, figures 3 and 4). A slightly intersexual male is shown on Plate 12, figure 8. In this species increasing degrees of intersexuality gradually change the colouring from the female to the male type; in male intersexuality, however, the female colour-pattern appears as patches upon the wings, as in the illustration.

Haldane has pointed out that when one sex of a hybrid, between races or species, is abnormal, rare or absent, it is the heterogametic one whichever that may be. This is due to the fact that in the homogametic sex the quantities both of male- and female-determining material is an average between that of the parental races. In the heterogametic sex, on the other hand, this is true only for the genes in the autosomes and the pairing region of the sex-chromosomes, while those balanced against them in the differential segment of the single X-chromosome are of one parental race only. Consequently in racial crosses the heterogametic sex must be less well adjusted than the homogametic one. For example, the cross between males of the Early Thorn, *Selenia bilunaria* Esp., and females of the Purple Thorn, *S. tetralunaria* Hufn., Selidosemidae, produces either male progeny only (Plate 31 and XIII) or a heavy excess of males.

The Gypsy Moth is now very rare in England. It used to occur commonly in the Fens, but has been extinct there since about the middle of the last century, and it may possibly have been introduced in the first instance. Only occasional specimens are now reported from time to time, though the species is frequent in southern Europe and a serious pest in some countries. However, intersexuality may be looked for among the offspring of any cross between geographically isolated races, and instances of its occurrence will be given on pages 173-175. They indicate that such forms have been evolving independently and building up distinct genetic constitutions, leading on to the production of new subspecies.

It will be appreciated in view of the numerical relationship indicated on pages 40-1, that the possibility of obtaining hybrid offspring may vary with the direction of the cross. Thus it is easy to produce hybrids by mating a male Eyed Hawk, *Smerinthus ocellatus* L., with a female Poplar Hawk, *Laothoe populi* L., Sphingidae, but not from the reverse pairing. There are many instances, however, in which a mating between different species, even when referred to distinct genera, leads to the production of hybrids of both sexes, though these are usually sterile or of poor fertility. Examples of this kind are shown on

Plate XIII. The Rannoch Brindled Beauty, *Poecilopsis lapponaria* Bsd., Selidosemidae, has a fully winged male and an almost wingless female (figures 3 and 5); so has the Belted Beauty, *Nyssia zonaria* Schiff. (figures 4 and 7). They can be successfully paired to give offspring of both sexes, of which a male is shown (figure 6), if *zonaria* be the male parent; if it be the female one, a great excess of male progeny is produced. These species can be crossed with the Brindled Beauty, *Lycia hirtaria* Cl., which is fully winged in both sexes (figure 8 male, 9 female), and both male and female hybrids result (*lapponaria* × *hirtaria* figures 10 male, 11 female; and *zonaria* × *hirtaria* figure 12 male, 13 female). It will be noticed that the hybrid females are approximately intermediate between the respectively fully winged and apterous condition of that sex in the two parental species. In moths, all stages are encountered between hybrids that are sexually perfect in both sexes, through that with normal males and abnormal females, to one in which males only are produced which, in the extreme situation, may be highly intersexual.

Hybrids in the Lepidoptera have been insufficiently examined from the genetic point of view. It is a remarkable fact, to be explained on pages 50-1, that they sometimes possess characters absent from both their parental species. Such instances, which do not seem to have been reported in this group, would certainly be worth careful investigation if found.

SEX-LINKAGE

Autosomal linkage has been discussed in the preceding chapter. Genes situated in the sex-chromosomes are distributed relative to the sex-determination mechanism and are therefore said to be *sex-linked.* They can evidently be carried in three ways: in the differential region of X, in that of Y, or in the pairing region interchanged between X and Y.

When sex-linkage is mentioned without any qualification it always refers to total sex-linkage in X, due to genes in the differential region in that chromosome. These are therefore distributed strictly in association with the sex-determining agents. Some of the results to which this gives rise were outlined in the previous volume of this work, but since the phenomenon has not yet been detected in butterflies it was treated very briefly, using an example drawn from moths. The

1
OXFORD

2
ORTON,
CUMBERLAND

3
Female,
OXFORD

4
Male,
BUCKINGHAM

5
OXFORD

6
THURSBY,
CUMBERLAND

7
THURSBY,
CUMBERLAND

8
OXFORD

1. Red Underwing, *Catocala nupta;* 2. Large Yellow Underwing, *Triphaena pronuba;* 3 & 4. Winter Moth, *Operophtera brumata;* 5. Turnip Moth, *Agrotis segetum;* 6. V-Moth, *Itama wauaria;* 7. Antler, *Charaeas graminis;* 8. Goat Moth, *Cossus cossus*

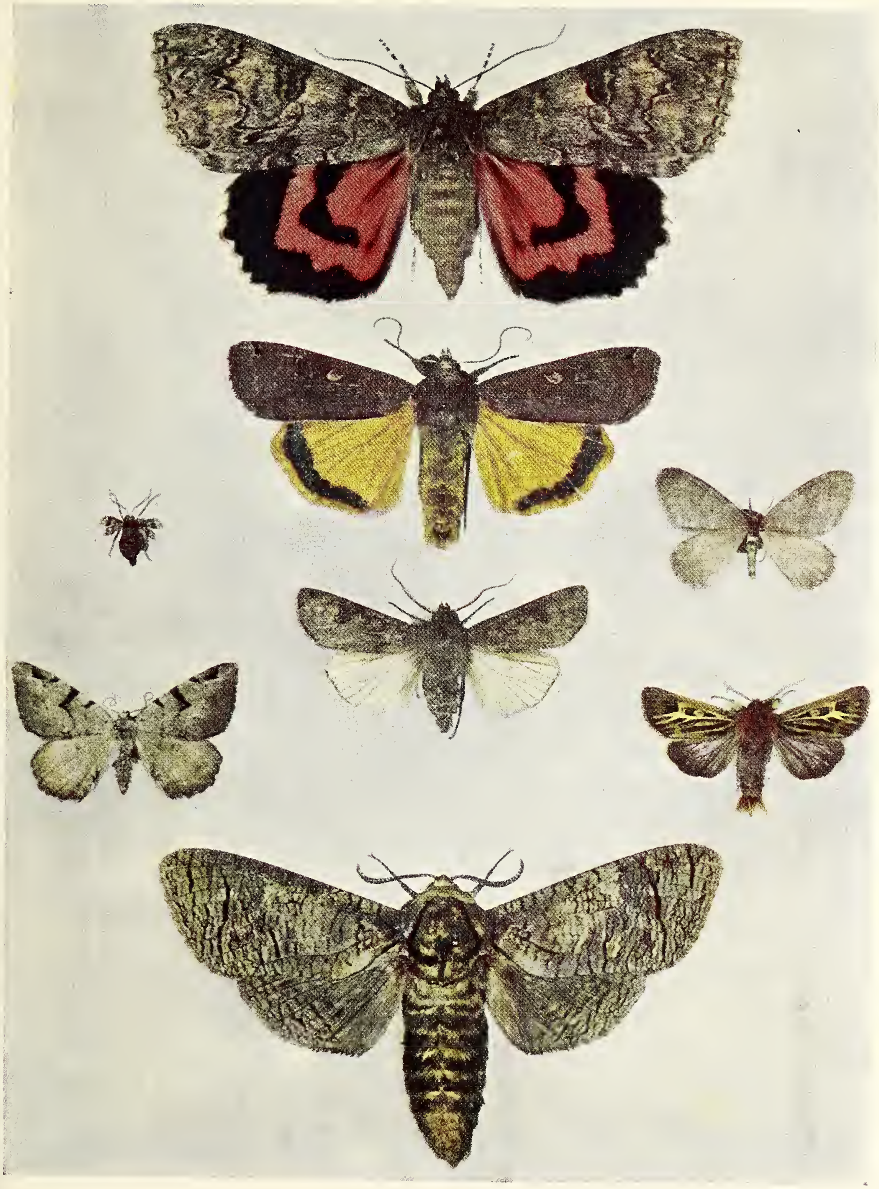
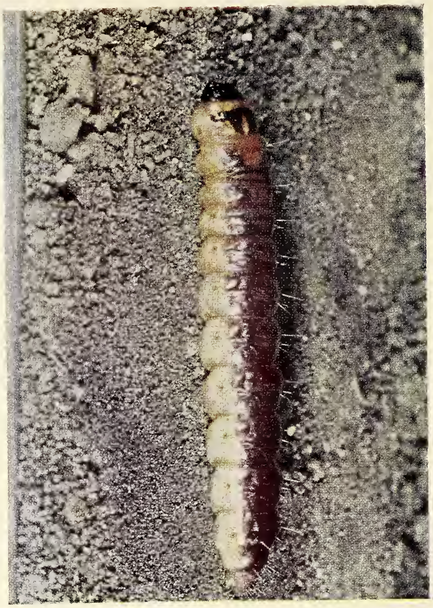
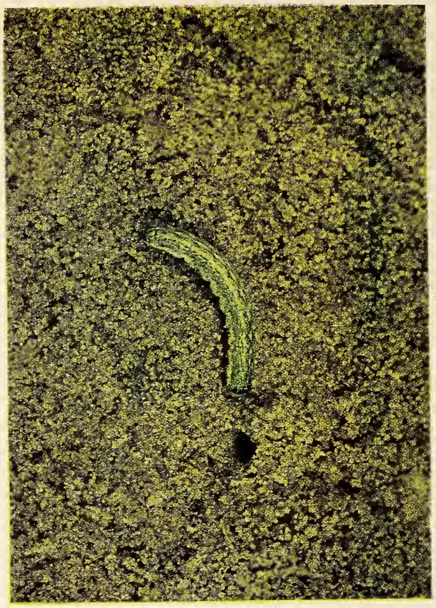


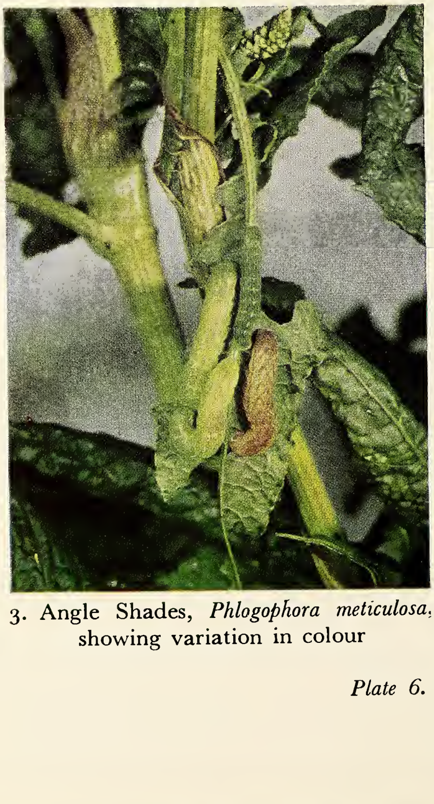
Plate 5



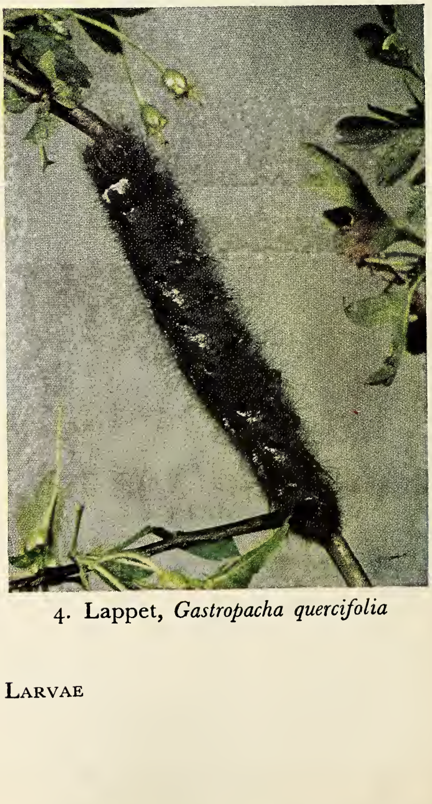
1. Goat Moth, *Cossus cossus*



2. Portland Moth, *Actebia praecox*, at entrance to burrow



3. Angle Shades, *Phlogophora meticulosa*, showing variation in colour



4. Lappet, *Gastropacha quercifolia*

Plate 6. LARVAE

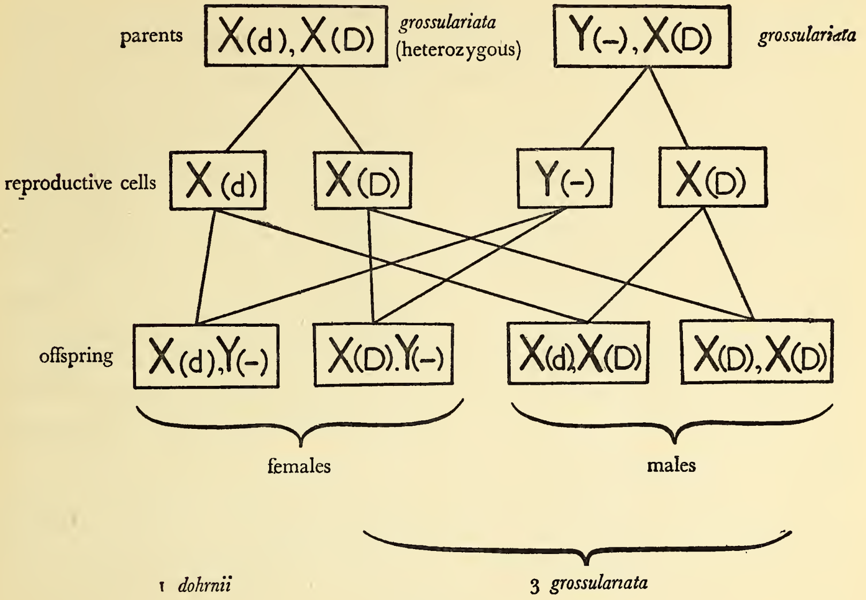

parents
X(d), X(D)
grossulariata (heterozygous)
Y(–), X(D)
grossulariata
reproductive cells
X(d)
X(D)
Y(–)
X(D)
offspring
X(d), Y(–)
X(D), Y(–)
X(d), X(D)
X(D), X(D)
females
males
1 dohrnii
3 grossulariata

FIGURE 3

Mating between a normal female Currant Moth and a male heterozygous for the recessive gene *dohrnii*, which is totally sex-linked to the X-chromosome

one selected was the pale variety *dohrnii* of the Currant Moth (Plate XII, figure 1, *grossulariata*, figures 4-5, *dohrnii*) the analysis of which, by Doncaster and Raynor in 1906, led to the discovery of sex-linkage. At that time it was known as *lacticolor*, this being one of the many instances in which a historic name has unwisely been changed to conform with the rules of priority. Total sex-linkage in X must now be explained more fully, and this original instance can still be used to illustrate it.

Dohrnii is a recessive variety, so that heterozygous males are of normal appearance. They can be represented as X(D), X(d), to indicate the carriage of this gene in the differential region of the X-chromosome. That of Y is genetically distinct from it and contains no loci allelomorphic with those in X. Therefore female Currant Moths, which have but a single X-chromosome, possess only one of the *dohrnii* genes. This may be either D or d. In the latter event the insect is *dohrnii*, since the action of the single recessive (d) cannot be obscured by a normal (dominant) allelomorph carried in Y. A female carrying X(D) is of course ordinary *grossulariata*, and the cross between such a specimen and a heterozygous male can be represented as X(D) Y(—) mated with X(D) X(d). Here the chances are equal that the Y-chromosome assorts with an X carrying D or d, so producing normal females Y(—) X(D), and *dohrnii* females Y(—) X(d) in equality; also that the equally numerous X-chromosomes carrying D, derived from the female, assort with X(D) or X(d) supplied by the male to produce X(D) X(D) and X(D) X(d), also in equality. These two classes are both male *grossulariata*, one homozygous and the other heterozygous. That is to say, all the males and half the females are normal *grossulariata*, so that *dohrnii* affects one-half of the male offspring only. This is a 3: 1 ratio, but one related to sex. It is represented diagramatically in figure 3.

By working out the combinations in the same way as is done in figure 3, it will be found that a pairing between a *dohrnii* female, X(d) Y(—) and a heterozygous male X(D) X(d) gives rise to all four classes in equality: X(d) Y(—), X(D) Y(—), *dohrnii* and *grossulariata* females; X(d) X(d), X(D) X(d), *dohrnii* and heterozygous *grossulariata* males. That is to say, *dohrnii* is not restricted to one sex though it is much commoner in females than in males. It is easy to see why this should be so. Since the Y-chromosome does not carry the *dohrnii* allelomorphs, the pairing region of X has no partner in the female, so that a single dose of the recessive must always exercise its effect in that sex, but two doses are necessary for it to do so in the male. A mating between a *dohrnii* male and female naturally produces a family which are all of this variety and breed true for it.

The distribution of the three genotypes in a population mating at random has been given for the autosomes on page 25. It can also be stated for sex-linkage. If p be the fraction of female moths in a wild population which shows a totally sex-linked character, the fraction of males which do so is p^2. Thus the ratio of such females to males is 1 : p. Therefore when a sex-linked recessive is found in one female moth in a thousand, it will occur in one male in a million. If on the other hand the mutant were a rare dominant, it would be approximately twice as common in males, with two X-chromosomes, as in females with one, for the homozygous dominants would occur so seldom that their frequency would be negligible. The only instances of the kind known to me in the Lepidoptera are provided by the melanism of the Black Arches, *Lymantria monacha* L., which is due to the action of three genes, all dominants, one of them sex-linked and two autosomal (page 190), and by the banded form of the Autumnal Moth, *Oporinia autumnata* Bork., Hydriomenidae, which is an almost complete dominant.

Only one gene apparently situated in the differential segment of Y has so far been detected in the Lepidoptera. This produces a black female form of the Pale Brindled Beauty, *Phigalia pilosaria* Schiff, Silidosemidae. All its female offspring are black and all its male offspring normal: a result that is constantly repeated in subsequent generations. The normal males do not transmit the gene concerned. (It may be noted, however, that there is another and much commoner black form of this moth which is inherited as an ordinary autosomal dominant and affects both sexes).

It will be realised that genes carried in the non-pairing region of the Y-chromosome give rise to a most exceptional condition, being transmitted down the female line in the Lepidoptera. Consequently, it is difficult to distinguish them from those rare genes which are maternally inherited because carried in the cytoplasm. In the majority of animals, in which the sex-determination is the other way round, this confusion could not arise, for the male contributes a negligible amount of cytoplasm to the offspring. It is of course easy to distinguish total sex-linkage in Y from *sex-controlled* inheritance (pages 60-2), in which autosomal genes express their *effect* in one sex only, for these are transmitted equally by both sexes. Such autosomal genes can therefore be inherited through the homogametic sex, which is not normally possible for a gene restricted to the Y-chromosome.*

Partial sex-linkage is due to genes situated in the pairing region of X and Y, and therefore interchangeable between them as a result of crossing-over. Several diseases in man are inherited in this way; for instance, xeroderma pigmentosum and retinitis pigmentosa.† These differ from total sex-linkage in either X or Y in two respects: first, such genes have two allelomorphs in both sexes instead of in the homogametic one only; secondly, as already indicated, they can be transferred between X and Y.

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*The existence of occasional XXY individuals provides rare exceptions to this statement.

†Other genes, one totally sex-linked and the rest autosomal, also give rise to this latter condition.

Consider the inheritance of a recessive partially sex-linked character. The specimens possessing it must receive the gene responsible for it from both their parents. In the male this must have been in the X-chromosome, in the female it may, with equal probability, have been in X or Y. If no crossing-over occurred, half the female but none of the male progeny would be affected if the gene were carried in the maternal Y, but the reverse would be true if it had been in the maternal X. But crossing-over can interchange such a gene from one maternal sex-chromosome to the other, from X to Y or the reverse, so leading to exceptions: that is, to the appearance of occasional recessive males on the one hand, or recessive females on the other.

There is a strong suggestion that several varieties are inherited in this way in moths, though in none of them has partial sex-linkage been established beyond doubt. For instance, H. B. Williams has bred the yellowish form *haggarti* of the Willow Beauty, *Cleora rhomboidaria* Schiff. (Selidosemidae), shown in its normal and melanic forms on Plate XXIV, figures 8 and 9. His results indicated that *haggarti* behaved as a normally sex-linked recessive, except that the stock originated from a wild female *haggarti*, captured in Ayrshire, which produced five males, all *haggarti*. This is a most improbable result if the gene were situated in the differential segment of X, but not unexpected if it were in the pairing region of X and Y.

Partial sex-linkage is generally confused with autosomal inheritance when the results of a number of different broods are combined, for the association with sex is then obscured. It will be found, however, that in some families there is a significant excess of female varieties and in others of males, to a corresponding degree. This cannot be the result of sex-controlled inheritance since, when the records of various families are combined, the sex-ratio of such forms will not depart significantly from equality.

A study of partial sex-linkage has provided the only opportunity that has so far arisen for constructing a genetic map of any part of the human chromosomes (see Ford, 1948). It would be well worth while to search for the phenomenon, and to exploit it from a corresponding point of view, in the Lepidoptera.

CHAPTER 4

GENETIC INTERACTION

Factor Interaction

It is usual to follow the segregation of a gene by tracing through several generations the appearance of some well-marked character to which it normally gives rise. Consequently there is some danger of thinking of the hereditary material as made up of units each of which acts in a single and specific way. That is a great over-simplification of genetics, one which obscures its working and the opportunities for evolutionary adjustment which it provides. In fact the genes each have many effects, and they interact with one another and with the environment to produce the characters for which they are responsible. A study of this aspect of the subject is one of the less frequent tasks undertaken by geneticists, and it has certainly received little attention in the Lepidoptera. Yet the character by which we find it convenient to mark the presence of a particular gene may by no means be the most important which it controls. For example, nearly all the mutant genes studied in this, or any other, group of organisms reduce to a varying extent the health and vigour of the individual. That is to say, they must influence the body in ways unknown to us. The extraordinary circumstance that a few mutant genes, those used, or capable of being used, in the production of industrial melanism (pages 194-6), actually confer superior hardiness upon their possessors, is evidence of the same fact; for the question why they have therefore remained mutants, and have not displaced their less viable normal allelomorphs, is not relevant to this part of the discussion, important as are its evolutionary implications. That at least the ‘ major ’ genes (page 55) so constantly affect viability, and to an extent which we are able to detect, suggests that their action is nearly always multiple.

This generalisation is sufficient for our purpose. Consequently we are not much handicapped by the fact, already mentioned, that in the

Lepidoptera no thorough studies have been made of the diverse effects of single genes, such as have been undertaken in some other organisms; *Drosophila melanogaster* for instance. Indeed specific instances of genes controlling several different characters in moths have only accumulated incidentally in the course of other work. An interesting example is provided by the results of P. M. Sheppard who studied the three forms *dominula*, *medionigra* and *bimacula* of the Scarlet Tiger, *Panaxia dominula* L., Hypsidae. These are under unifactorial control, *medionigra* bring the heterozygote, yet they differ from one another not only in their wing-markings (Plate 11, figures 1-5) but in their mating habits. Indeed research on the genetics of habit is much needed. Its hereditary control must be of great importance in evolution, but very little is known of the subject. I add here a remarkable instance drawn from butterflies, since it was not known when I wrote the first volume of this work. W. Hovanitz, working on the American *Colias philodice*, Pieridae, has shown that the gene responsible for changing the colour of the females from the normal yellow (recessive) to whitish (dominant) influences also the activity of the insect: the white females are more active than the yellow in the early morning and towards evening. An example of a very different kind is supplied by var. *brevipennis* of the Scalloped Oak Moth, *Crocallis elinguaria* L., Selidosemidae, already mentioned (page 23), in which the markings and the neuration of the wings are modified by the same gene.

Not only do the genes have multiple effects but they interact with one another to produce them. This statement is based both upon our general knowledge of their working in animals and plants and upon a study of the results produced by the segregation of two or more of them in the same organism. Unfortunately this is an aspect of genetics about which very little is known in the Lepidoptera, so that it must be illustrated principally from other animals.

In the fly *Drosophila melanogaster* a mutant gene, when homozygous, changes the normal dominant red eye-colour to brown, while another turns it scarlet; yet the two homozygous recessives combine to produce white eyes. A more striking instance is provided by an inter-generic cross in Cyprinodont fish. A gene produces dominant black spotting in *Platypoecilus maculatus*. When the non-spotted form is crossed with *Xiphophorus helleri* the hybrid offspring are quite healthy. However, if the spotted form be used, the action of the gene for black spotting is no longer properly adjusted in a genetic setting to which it is unaccustomed, one in which half the hereditary material is derived from another genus, and it then results in the formation of melanotic growths* which kill the fish.

An account will be given in Chapter 14 of experimental work in which the effect of a gene has been changed by selection. This operates on the genetic variability of the organism supplied by the rest of the hereditary material. The interaction of two genetic varieties in the Currant Moth, *Abraxas grossulariata* L. Selidosemidae, is shown on Plate XII; figure 7 represents the form produced when the pale variety *dohrnii* (figure 4) is combined with the melanic var. *varleyata* (figure 6), both of which are recessive.

P. Bovey has reported an instructive instance of the interplay of two genes in the Burnet Moth, *Zygaena ephialtes* L. This species is widespread in Continental Europe but does not extend to Britain. It exists in two principal forms.

1. *ephialtes.* This is a blackish insect with either five or six spots on the fore-wings and one or two on the hind. Red and yellow pigment is restricted to a band on the body and to the two basal spots on the fore-wings, the others being white.

2. *peucedani.* In this phase the red or yellow colouring extends to all the spots on the fore-wings and occupies also the basal area of the hind-wings.

Red pigmentation is a simple dominant to yellow, and *peucedani* is dominant to *ephialtes* except that the heterozygotes are more variable than the dominant homozygotes. These genes are not linked.

Almost all the specimens are *peucedani* in the West (France) and *ephialtes* in the South (Italy), but the two occur together over the greater part of the insect's distribution. Red and yellow *ephialtes* may be intermingled, but in some places (Cyprus) only the red is found, and in others (Peninsular Italy) only the yellow. It is clear therefore that either form or either colour may be at an advantage in nature. However, the genes for the dominant *peucedani* pattern and the recessive yellow colouring interact in a disadvantageous way, for yellow *peucedani* are rare and local and are found only in a few places in Central Europe where red and yellow *ephialtes* and red *peucedani* form a mixed population.

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*These are not malignant (" cancerous ") for apparently they do not metastasize.

Continuous Variation

The interactions so far mentioned take place between genes which have very different effects from one another. A study of those producing closely similar or apparently identical characters would contribute information of importance on the way which the hereditary material controls variation. It is unfortunate that in the Lepidoptera examples of this kind have seldom been investigated in detail.

In the Currant Moth (Plate xii, figure 1) the sex-linked recessive *dohrnii* greatly reduces the spots on the upper-side of the wings (figure 4) and almost obliterates those below (figure 5). Another variety, also a simple recessive but autosomally inherited, is almost identical above (figure 2) but the under-side pattern, though reduced in intensity, is preserved (figure 3). It is likely that the chain of reactions between gene and character is rather similar in these two mutants. A somewhat parallel instance is provided by two closely allied species of the genus *Oporinia*, Hydriomenidae. The banded form of *O. dilutata* Schiff., the November Moth (Plate xii, figures 8 and 9) is an autosomal dominant, while that of *O. autumnata* Bork., is sex-linked and its dominance is nearly but not quite complete. Moreover, in the latter species the banding is less heavily developed. It is improbable therefore that it is due to corresponding mutations of the same gene, derived from the common ancestor of these two moths. Its different type of inheritance (sex-linked and autosomal respectively) is strongly opposed to such identity but does not absolutely exclude it, since fragments can occasionally be interchanged between different chromosomes (' translocation '), carrying their genes with them. The corresponding banded form of a third closely related species *O. christyi* Prout (figures 10 and 11), is not a sex-linked recessive, but its further analysis awaits investigation. A more instructive example of two genes producing a similar form of variation is supplied by melanism in the Mottled Beauty, *Cleora repandata* L., Selidosemidae (Plate xxiv, figures 6 and 7). The black varieties to which they each give rise are identical in appearance and both are unifactorial. What then is their relationship? First, they are not multiple allelomorphs, since an individual homozygous for one carries the allelomorphs of the other; secondly, one is dominant and the other recessive. Now since dominance and recessiveness are the result of selection (pages 214-15, see also *Butterflies*, pages 257-262), the two genes concerned must produce the melanism for which they are responsible by somewhat different means, otherwise the same character could not in the same individuals be adjusted in different ways. Moreover, it is only in their effect on colour-pattern that these two genes are alike. Their influence upon the vital processes of the body, upon its physiology, that is to say, are distinct; for the dominant melanics are hardier than the normal individuals (page 195), while the recessives are much more delicate. Here then we have good evidence that the reactions initiated by these genes, and presumably the genes themselves, are different from one another. It is only in circumstances such as these, rarely analysed so far, or when interspecific hybrids can be produced, that it is possible to contrast the working of two genes having similar effects.

In the instance just quoted, the two genes for melanism when brought together into the same individual do not reinforce one another. Similarly, Heslop Harrison combined the melanism of the two species of Engrailed Moths; that of *Ectropis crepuscularia* Hb., Selidosemidae (Plate XXIV, figure 10 normal, 11 melanic), in which it is dominant, and of the darker form of *E. bistortata*, Goeze (Plate 31, figure 5 normal, 6 melanic), in which it is recessive, by producing hybrids between them. It will be seen that these varieties are not alike, that of the latter species being much the darker. The genes producing them do not act cumulatively, for the double homozygotes which he was able to obtain are merely of the black *bistortata* type. This, however, may be due to the fact that the amount of melanin has in this form approximately reached saturation as far as its visible effect is concerned, so that a considerable addition to the quantity of pigment would not alter the intensely dark colour already present. One could dilute considerably a bottle of ink by adding water to it without appreciably altering its shade. On the other hand, the fact that some genes have large yet similar effects, prepares us for the situation in which those responsible for less marked changes are often additive in their action.

The melanism of the Black Arches, *Lymantria monacha* L. (Plate XIV, figures 1 to 6), is due to three genes which reinforce each other. The blackest specimens carry all three, but they are not of equal importance, one of them, a sex-linked dominant, having much the greatest effect. However, the melanism of the November Moth (Plate XIV, figures 7 to 10) is, in Southern England at any rate,* due to a large number of genes whose action is small and additive. Thus if a normal and a black specimen (figures 7 and 10) be crossed, the F_1 offspring are of an intermediate shade, while when these are interbred the F_2 generation so produced consists of insects ranging almost from normal on the one hand to the fully melanic on the other. The colours are so distributed that the extreme light and dark individuals are rare and the intermediates are common. Indeed if the numbers be plotted against the degree of darkening, the result is a bell-shaped 'curve of normal distribution' of the type always obtained when variation is due to a large number of components (in this instance, hereditary units and environmental effects) each of which has an average value and varies round it independently: as in human height when we consider a fairly homogeneous* adult population of males or females, as found in most English towns.

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*A gene with a marked effect may be responsible for melanism in Northern England.

'Continuous variation' such as this is not divisible into separate classes like the discontinuous type produced by the segregation of one or a very few pairs of allelomorphs. That is to say, the *character* concerned is a blend between the extreme parental or grand-parental types. Yet we have complete evidence that the hereditary units do not blend also, but remain perfectly distinct, and that the members of each pair of allelomorphs concerned undergo segregation: as a result, they obey the fundamental laws of 'particulate' heredity. For blending leads progressively to uniformity: that is what we mean by blending. Consequently under its influence the F_2 generation would be less variable than the F_1. That the reverse is true demonstrates that continuous variation is due to genes which retain their identity; though the classes produced by their segregation are not separately distinct, owing to the fact that they differ only quantitatively and overlap.

There is no fundamental genetic difference between discontinuous and continuous variation; indeed, the latter must in general be far the commoner type, though it has been much less studied. Another instance of it which has been analysed in the Lepidoptera is provided by the size of the Marsh Fritillary butterfly, *Melitaea aurinia*, as measured by wing-expanse. When a large specimen was crossed with a small, both the F_1 and F_2 generations obtained from them were of intermediate dimensions, but the F_2 specimens were more variable than the F_1. In the previous volume (*Butterflies*, pages 222-3) such

*One in which races with very different average heights are not mixed.

' multifactorial ' inheritance was also illustrated by reduction in the spotting of the Ringlet, *Aphantopus hyperanthus*.

It should be noticed that some genes are only concerned in producing small additive effects. Thus they are to some extent of a distinct type. These are the ' polygenes ' and they can be carried in all parts of the chromosomes. The ' major ' genes, those whose action is more marked, so that they tend to produce classes sufficiently distinct to be scored separately in segregation, are situated only in certain so-called ' active ' regions of the chromosomes: in contra-distinction to the ' inert ' segments. These were formerly supposed to be destitute of genetic material, but are now known to carry polygenes.* It will, of course, be appreciated that among the various effects to which each major gene can give rise some may be small and act cumulatively. Thus some of the characters produced by ' major ' genes are like those due to polygenes.

ENVIRONMENTAL VARIATION

It has already been suggested that the fluctuating influence of the environment will tend to produce continuous variation, co-operating with the polygenes in the process. Now the genes interact not only with one another but with the environment in which they work. Indeed heredity and environment are to an approximately equal extent responsible for the variation normally to be seen in animals and plants.

The action of the genes depends upon the environment in which they are placed: alter it and their effects may be changed, restore it and the original condition will be recovered. The environment of a gene should properly be considered at three levels: (i) the external environment of the organism: that is to say, the temperature and humidity to which it is exposed, the type of food which it eats, or the visual stimuli which it receives; (ii) the physiological environment of the body, depending, for instance, upon the different secretions circulating in the blood; and (iii) the other genes with which it interacts to produce its effects. The last of these aspects has now briefly been discussed. The other two require at least some mention.

Several examples of environmental variation were given in *Butterflies* (pages 240-247). It is likely that the characteristic differences between the spring and summer broods of moths, which must be environmental, are controlled directly or indirectly by the temperature, but the subject has been very little studied experimentally. For example, the second brood of the Maiden's Blush, *Cosymbia punctaria* L., Sterrhidae (Plate 14, figure 9 first brood, figure 10 second brood), has consistently a series of blotches in the distal area of the fore-wings, absent from the first brood specimens. When an exceptional third brood is reared in captivity in the autumn, it is marked like the second one, so that no type of alternating rhythm is involved, the mechanism of which would indeed be hard to envisage. On the other hand, the difference in size between the spring and summer broods of some species, such as the Small Square Spot, *Diarsia rubi* View., Caradrinidae, in which the early specimens are the larger (Plate 14, figure 11 first brood, figure 12 second brood), may well be connected with the length of larval life: those which produce the second brood insects feed up more rapidly.

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*In the active chromatin the coating of nucleic acid is depolymerised and broken down at telophase, while in the inert region it is retained.

Our knowledge of the effects of temperature on the colour-pattern of moths has been much extended by the work of Kettlewell on the Bordered Straw, *Heliothis peltigera* Schiff., Caradrinidae. His studies were planned with care and have accordingly supplied precise information. He finds that the pupal life of this and presumably of other species can be divided into two phases. First, a period of rest following the destruction by phagocytosis of the majority of the larval tissues. This may vary between different species from a few days to several years, and at least in the Bordered Straw the temperature changes which take place during it have no effect upon the colour-pattern. It is followed by an active phase of reconstruction and differentiation. When this is accelerated by heat (30° C.), the amount of pigment which can be laid down in the wings is small, and the specimen is pale and lightly marked. But when prolonged by cold (6° C.), the quantity of pigment deposited is large, and the insect is heavily marked and dark. In the earlier part of the active phase the pigment of the pattern is laid down, in the later part that of the ground-colour. Thus by an appropriate temperature-control, pale specimens lightly or more heavily marked (Plate 14, figures 5 and 8), or dark specimens with obscure or clear markings (figures 6 and 7) can be produced. Those figured* are among the insects bred in these experiments. Temperature, then, principally acts by controlling the lengths of the two parts of the active phase of pupal life, and presumably therefore the period during which the scales are in a condition to take up pigment (see *Butterflies*, pages 43-4, for an account of the timing of scale-development in relation to pigment-formation). However, Kettlewell also obtained some indication of a direct temperature-effect upon the production of pigment itself, and doubtless this acts as another component in the system. With so complex a type of control, depending on the nature of the pigment, the time at which it is produced, and the rate of development of the scales, one would expect considerable variation in effect. Thus in butterflies, a heavy deposition of melanism is promoted by cold in the Vanessidi but by heat in the Pierinae.

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*They have been kindly lent from the Rothschild-Cockayne-Kettlewell collection of the British Museum.

The interplay of genetic and environmental agencies in controlling variation is well illustrated by some further temperature experiments, also conducted by Kettlewell, on the Scarlet Tiger, and illustrated here from specimens bred during the course of the work* (Plate 14, figures 1 to 4). Kettlewell discovered a mutant gene which produces an extreme dark variety when homozygous (figure 2). The heterozygotes (figures 3 and 4) are intermediate between it and the normal form (figure 1) but are the most variable of the three genotypes, the normals being the least so (page 22). Segregation, therefore, took place in a 1 : 2 : 1 ratio, but its effects were only detectable when the specimens were bred at a constant temperature of 21°±3 C. When reared at varying temperatures, ranging from 7° to 27° C., the visible effects of the gene were obliterated and all the mutant specimens, whether heterozygous or homozygous, were indistinguishable from normal *dominula*.

Further work on this remarkable form is needed to decide between two alternative conditions which may control it. It is possible that this gene ceases to act if the temperature falls appreciably below 20° C., and it may be that the critical period for producing its effects is a very brief one. Alternatively it may be that the specimens are ‘ buffered ’ against it in ordinary environments but not when bred at a constant temperature, this being a situation of which the species has no experience: that is to say, perhaps the gene could produce the characters for which it is responsible provided the insect were kept at any *constant* temperature within the range it can tolerate.

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*They have been kindly lent from the Rothschild-Cockayne-Kettlewell collection of the British Museum.

This latter alternative is indeed quite a possible one and draws attention to an important aspect of the adaptation of the organism, one which helps to explain why environmental variation is not more often encountered in genetic work. Manifestly it is to the advantage of all forms of life to maintain themselves as nearly as possible within their optimum range of conditions and therefore, incidentally, within a constant range, which may be wide in the more tolerant species but very narrow in others. This they may achieve in a great variety of ways: by migration from worse environments to better, or by manufacturing a favourable environment of their own and carrying it about with them. Thus the tissues of an insect are bathed in body-fluids which, at least on analogy with other organisms, are maintained at the correct hydrogen-ion concentration and osmotic pressure with great exactitude. To take an extreme instance from a very different group of animals, it is possible only to perform temperature-experiments of a most limited kind upon mammals since they live permanently at their own optimum temperature. In addition, many animals are so adjusted as to evoke their normal characters within the whole range of conditions to which they are habitually exposed. This is one of their noteworthy adaptations, produced by selection; but it of course fails to adjust them to those situations which they do not normally encounter. Both these tendencies obviously so work as to reduce the influence of the environment in causing variation.

A very curious and widespread type of dimorphism is the production of green compared with brown or blackish colouring in larvae and in some pupae also. It has been briefly discussed in *Butterflies*, page 247, and illustrated on Plate 2 of that work. Such variation has been reported in a great many species widely scattered among the Lepidoptera. It is by no means fully understood and has indeed never been subjected to the rigorous experiments which would be needed to interpret it. There is some suggestion that this colour-difference is partly controlled by temperature, but there seems also confirmation for the view that it is due principally to visual stimulation acting on the larval ocelli, and so determined in advance for the pupal stage when this is affected. There are many reports that green and brown larvae habitually rest upon backgrounds which they match: leaves compared with twigs in the Pine Hawk, or the green and brown parts of the food-plant in such a species as the Angle Shades, *Phlogophora* *meticulosa* L., Caradrinidae, in which this form of variation is here illustrated (Plate 6).

These statements require to be confirmed by careful experimental work before they can be accepted. If indeed visual stimulation be responsible for the colour-adjustment, the tendency to rest upon different backgrounds will be the ‘ cause ’ of the variation rather than a consequence of it. Alternative green or dark forms of pupae are only found among those that are placed in exposed positions, and therefore depend upon their colouring for protection. Indeed the absence of such variation in subterranean pupae indicates that it has been specifically evolved, presumably for cryptic purposes. In those species in which this pupal dimorphism occurs, as in the Small White Butterfly or the moth genus *Cosymbia*, Sterrhidae, it should not be a difficult matter to determine statistically the relationship of pupal colour to background, although a certain number of specimens of intermediate shade may cause difficulty in scoring. The subject should also be attacked upon the lines used by Brecher (see *Butterflies*, page 247), who varnished the larval ocelli different colours and reported that the appearance of the pupa could be controlled by this means. It is likely that in some species the control is environmental and in others genetic.

It seems that work on this type of environmental variation, which is rather ill-defined and capricious, has been largely avoided by geneticists and physiologists. Data bearing on the subject are much needed, but some are now being obtained by Bowden and others.

Finally, it is necessary to discuss briefly the remaining aspect of the environment to which the genes are exposed; that provided by the body of the insect and varying according to its working or physiology. This determines which genes shall be operative in the different stages in the life-history, the larva or imago for instance, and how their action should be modified in each.

Here we touch upon one of the more intricate concepts of physiology, that of tissue differentiation. The problem is that all the cells of the body contain a complete set of genes. Those, for example, in the foot of a man, possess the hereditary material that is needed to control the development of the eye, those in the leg of a moth carry the genes that determine the colour of the wings. What then causes the correct genes to work in those cells where they are wanted and renders the others inoperative? We return to the fact that the characters of the organism, in the widest sense of that expression, are the joint product of heredity and environment. The protoplasm even of the fertilised egg is not of uniform composition but differs in its activity from one region to another: near or far from the path taken by the sperm in reaching the nucleus for example. Hence as the egg becomes subdivided into separate cells the nuclei carried into them contain sets of genes which are not subject to identical conditions. They thus produce diverse effects, which accentuate the environmental differences to which they are exposed. The appropriate action of the hereditary material in the cells of one part of the body compared with another, or in those of the larva compared with the imago, is a result of the distinct ' internal ' environments to which they are subject in space and in time.

Sex-controlled Inheritance

Among the greater physiological differences between one individual and another are those due to sex. It is indeed clear that a given gene is by no means working in the same environment in males as in females, so that it will not necessarily produce the same effects in them. It will be remembered (*Butterflies*, page 192) that in mammals the sex-genes determine only whether the sex-glands shall develop as testes or ovaries. These then produce a hormone which, circulating in the blood, decides the sex of the rest of the body. In insects, on the other hand, the sex of every part is controlled by the chromosome-balance of the cells composing it. Any sexual difference in the effects of the genes is therefore more directly a matter of physiological environment in the one group and of genetic interaction in the other. Since all the genes responsible for the correct development of the secondary and accessary sexual characters* of a male are present in the female and the reverse, their appropriate action is stimulated, modified, or prevented as may be necessary, by the internal environment of the body.

It is to be anticipated that the different internal environments provided by the two sexes will influence the action of certain of the genes not directly connected with the development of any of the actual

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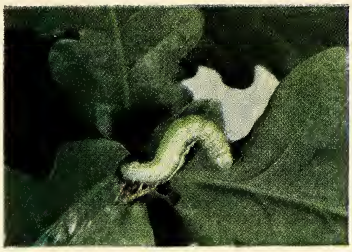
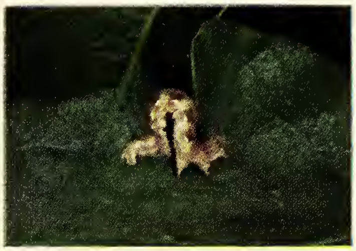
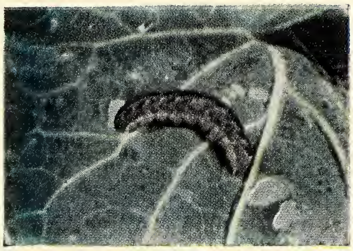
*The primary, secondary and accessary sexual characters are, respectively, the sex-glands themselves (testis or ovary), the structures concerned in the liberation or transfer of their products (vas deferens, oviduct, external genitalia), and the sexual qualities not directly connected with the act of reproduction (colour-pattern, for instance).



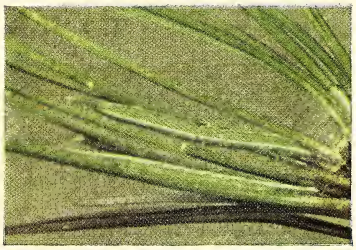
1. Dun Bar, *Cosmia trapezina*



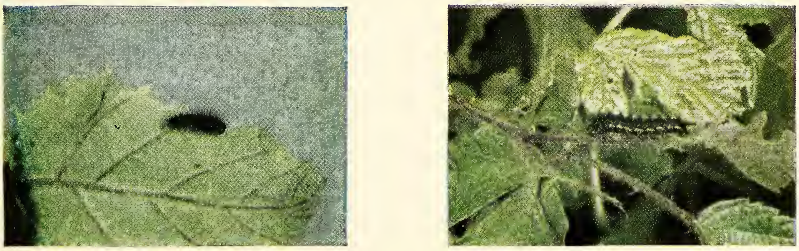
2. Mottled Umber, *Erannis defoliaria*



3. Cabbage Moth, *Mamestra brassicae*



4. Bordered White, *Bupalus piniarius*



5-6. Emperor, *Saturnia pavonia*, early stages

Plate 7. LARVAE

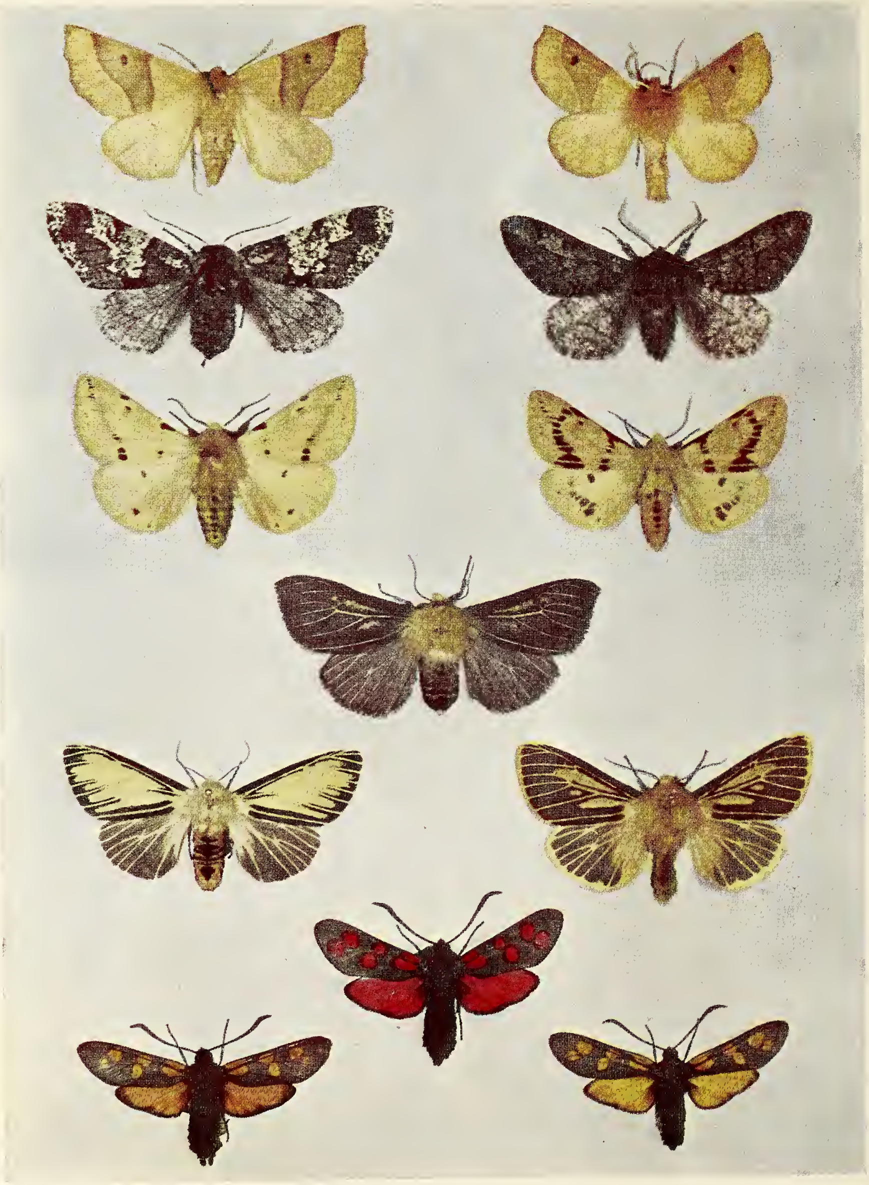


Plate 8

Plate 8. GENETICS: DOMINANTS AND RECESSIVES

1
CUMBERLAND

2
SKYE

3
CUMBERLAND

4
KENT

5
OXFORD

6
WOODWALTON,
HUNTINGDONSHIRE

7
YORKSHIRE

8
YORKSHIRE

9
YORKSHIRE

10
OXFORD

11
KENT

12
KENT

1 & 2. Scalloped Oak, *Crocallis elinguaria;* 1 typical, 2 var. *brevipennis;* 3 & 4. Oak Beauty, *Biston strataria:* 3 typical, 4 melanic; 5-9. Buff Ermine, *Spilosoma lutea:* 5 typical, 6 typical with enlarged spots, 7 var. *zatima* homozygote, 8 *zatima* light heterozygote, 9 *zatima* dark heterozygote; 10-12. Six-spot Burnet, *Zygaena filipendulae:* 10 typical, 11 salmon, 12 yellow

M F

sexual characters. That is to say, some genes may produce their effects only in one sex, though transmitted equally by either because situated in the autosomes. This is *sex-controlled inheritance.* It is to be distinguished from the sex-linked type in which a character is associated more often with one sex than with the other for purely mechanical reasons, because carried in a sex-chromosome.* Sex-controlled characters are not always completely restricted to one sex. Some genes produce their effects more often in males than in females, or the reverse. The fact that they are *transmitted* equally by both distinguishes this condition from sex-linkage.

Examples of single genes sex-controlled to the female were given in *Butterflies.* These were the pale female form *helice* of the Clouded Yellow, and the blackish female form *valezina* of the Silver-washed Fritillary. This condition is especially frequent in butterfly mimicry, which, however, is largely restricted to the sub-tropics and tropics. Rather curiously, but few instances of such sex-control have been reported in moths. It looks therefore as if they are related to the unusual requirements of mimetic species, a possibility which I have discussed elsewhere (Ford, 1953b).

Sex-controlled inheritance working in either direction can conveniently be illustrated from the Wood Tiger, *Parasemia plantaginis* L., Arctiidae. This is normally a black and yellow species (Plate 13, figure 5 male, 7 female), but in the males, though not in the females, the yellow colouring may be replaced by white, var. *hospita* (figure 6). This form is a sex-controlled dominant. On the other hand, some specimens are marked with red, due to sex-controlled inheritance in the opposite direction from *hospita,* for these are always females. It is said that they are simple dominants, but it will be desirable to confirm this conclusion with more extensive breeding work (see also pages 69-70 for a further account of these forms).

Moths, then, like other organisms are adjusted to their environment, in all senses of that term. Yet such adjustment cannot be obtained haphazard, but is the result of selection acting upon heritable variability in the manner which has been outlined in *Butterflies,* Chapter 12.

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*It is of course possible for a sex-linked character to be sex-controlled in addition, but no such instance is known in the Lepidoptera.

CHAPTER 5

POLYMORPHISM

THE THEORY OF POLYMORPHISM

ANY INSTANCE of polymorphism is a challenge to the naturalist just as it is to the student of evolution, for it advertises a situation that is bound to provide critical problems in the adjustment of a species to its environment and the means by which such adjustments are maintained: problems of the very type which the moth-collector, if he aims at something more than amassing representative sets, and varieties as curios, is well fitted to detect and to study. The existence of polymorphism is a sure sign that something of exceptional interest awaits investigation. Though in this book it would be quite inappropriate to attempt to list all the genes known in moths, it seems right to treat polymorphic variation somewhat fully in order to draw the attention of naturalists to precise instances which offer special opportunities for amateur work of scientific value.

I have defined polymorphism as the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation. This definition, which may appear somewhat formidable, clarifies the problem and indicates its essential features. In the first place, it excludes geographical and seasonal variation, for the forms must occur 'together' in the same habitat. Secondly, we are concerned with discontinuous variation, not with the 'continuous' type, whether under multi-factorial (polygenic) or environmental control. In a given locality a moth may have an intergrading range of forms falling within a curve of normal distribution. This is no more polymorphism than is the range of human height to be observed in the adults of either sex. Thirdly, it will be seen that the segregation of rare recessives, or of heterozygous forms normally eliminated by selection and maintained in the population only by mutation, does not constitute a polymorphism.

On the other hand, this definition includes two distinct conditions.

(1) *A Balanced Polymorphism* is that maintained by a balance of selective agencies which favour diversity and oppose uniformity. This usually results from the situation in which the heterozygote is at an advantage compared with either homozygote and from those systems which are so arranged as to promote out-breeding, such as sex itself, which is a true dimorphism, or the tendency for unlike rather than like varieties to pair (page 67).

(2) *A Transient Polymorphism* is produced by the temporary diversity which arises when a previously disadvantageous gene spreads through a population and displaces its allelomorph. This is usually due to a change in the environment or to a species colonising a new and distinct type of habitat. It will be reserved for discussion in relation to industrial melanism (chapter 13), since this produces the best and most striking examples of it, not only in moths but in the whole of the animal and plant kingdoms. The present section therefore will be restricted to a consideration of the balanced or permanent type.

A balanced polymorphism is possible only if some 'switch mechanism' has been developed capable of maintaining alternative forms in a single population. This is usually genetic and is achieved by the segregation of a pair, or a few interacting pairs, of genes. The environmental control of balanced polymorphism is very uncommon, because generally insufficiently exact and very liable to lead to the production of intermediates between conditions which should be sharply contrasted. However, an example of it in the Lepidoptera is provided by the alternative green and brown or blackish forms of some larvae and pupae which appear to be determined by visual stimulation (pages 58-9).

The members of a pair of allelomorphs may, at least in theory, be of unequal or equal survival value. The latter alternative is very rare, and for two reasons. First, it has been shown by R. A. Fisher that if the balance of advantages between two allelomorphs is effectively neutral, it must be remarkably exact and therefore very seldom attained. Secondly, if really of equal survival value, the rarer can spread and replace the commoner only at an exceedingly slow rate. That is to say, if derived from a single mutation, the number of individuals which

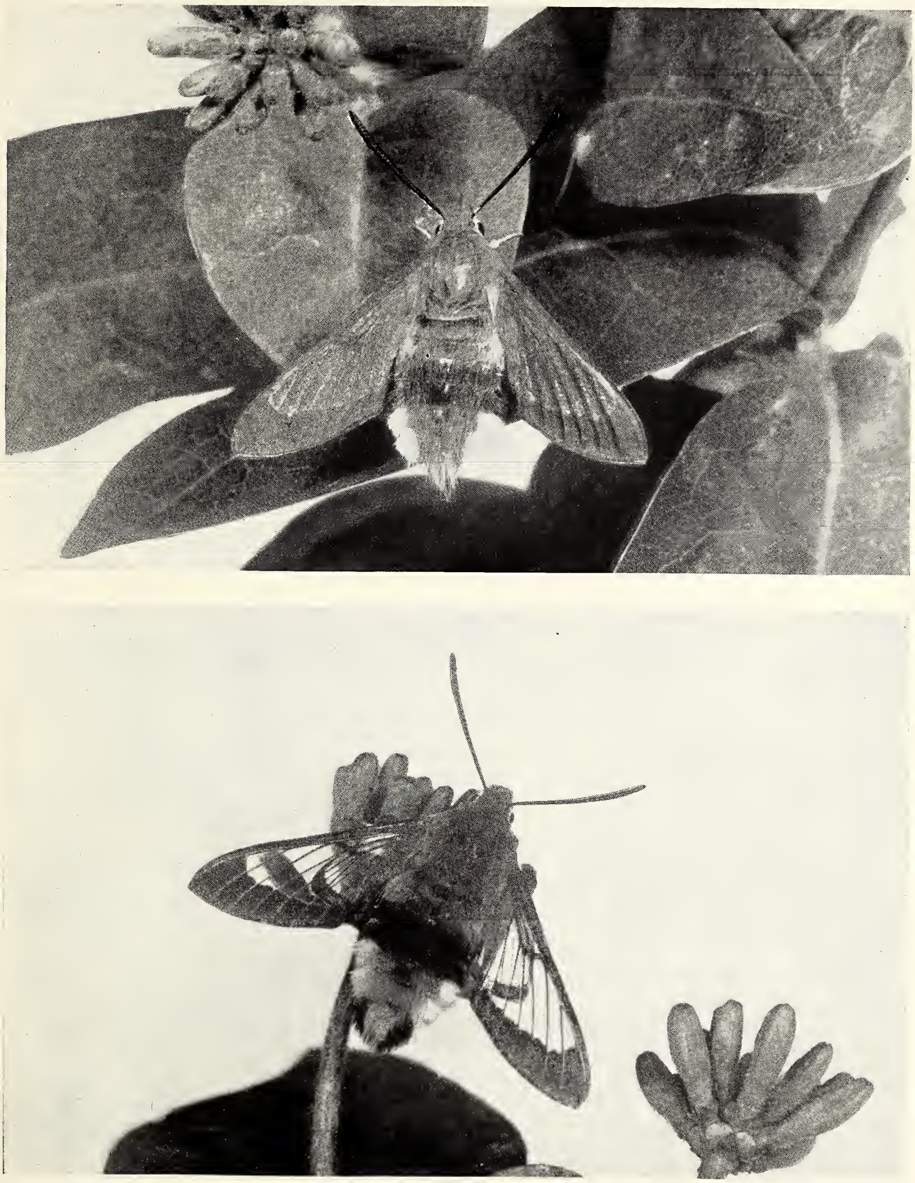
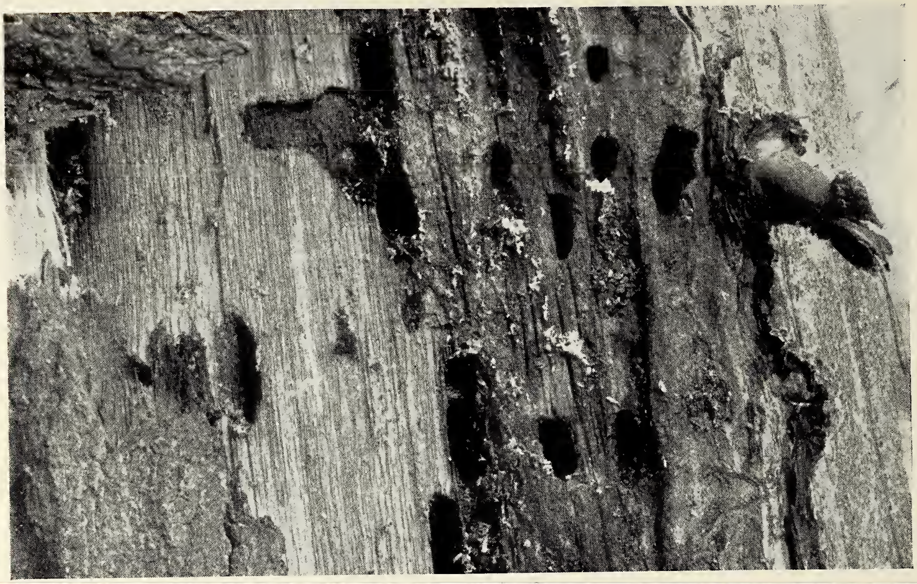


Plate V. Bee Hawk, *Hemaris fuciformis*, before and after Flight
1 (*above*). Before flight (X 2); 2 (*below*). After flight (X 2)



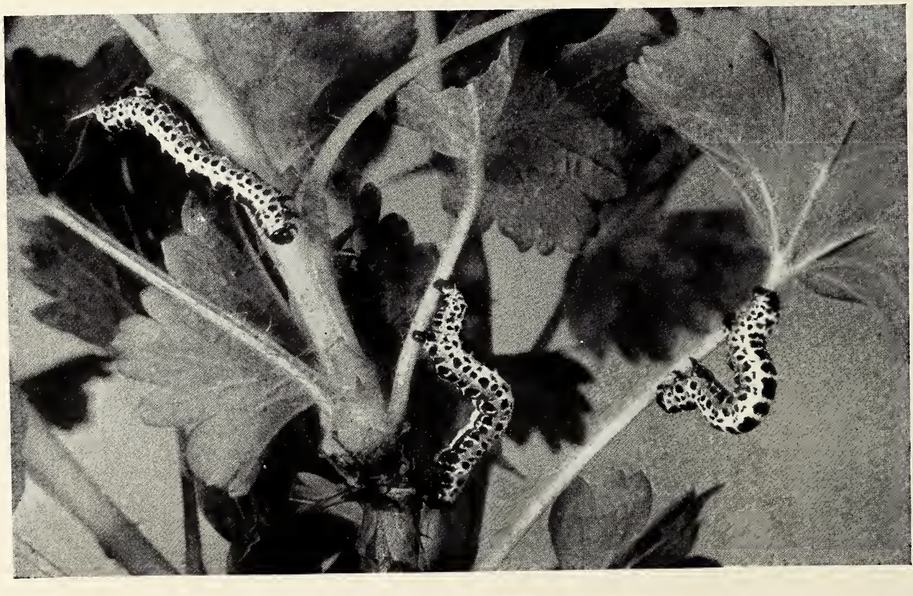


Plate VI. Injurious Insects

1 (*above*). Tree damaged by Goat Moth, *Cossus cossus*; 2 (*below*). Larvae of the Currant Moth, *Abraxas grossulariata* (X 1.5)

possess the gene cannot greatly exceed the number of generations since its occurrence; while the mutation-rate is too low materially to accelerate this process (page 33). Consequently the period of time involved is so great that the accurate balance of neutrality will almost certainly be upset long before a rare gene of this type has made any considerable advance towards becoming common. The result of these two deductions is this: that if the rarer of two allelomorphs has a heterozygous effect, it must almost certainly be of advantage to its possessor should it occur even in one per cent of the population; if recessive, the same will be true if the gene occupies much less than eighteen per cent of loci (a level ensuring that homozygous recessives comprise one per cent of the individuals).

Yet if such an advantage is maintained, the gene in question will gradually spread through the population and eventually reduce the form controlled by its once common alternative allelomorph to the status of a rare variety. That is to say, it will give rise to polymorphism of the transient type. The diversity so produced can be permanent, and the polymorphism *balanced*, only when an advantage decreases and is actually converted to a disadvantage as the form possessing it becomes relatively commoner. Selection will in fact secure that the proportion of the two or more phases of a balanced polymorphism will be so adjusted that they are all of equal advantage. It is not to be expected that this point of equilibrium will be the same in all conditions; by its very nature it will be sensitive to genetic and environmental changes. Consequently the frequencies of polymorphic forms will tend to vary from brood to brood and from one locality to another. That is to say, though seasonal and geographical variation does not constitute polymorphism, it may affect it.

If polymorphism is controlled by a single pair of genes and equilibrium is reached when one of them is rather rare, occurring in a few per cent only of the population (or, more correctly, occupying but a few per cent of the loci available for it), the result is effectively a dimorphism due to the segregation of a heterozygote and one homozygote. For the other homozygote will then be so exceedingly uncommon (page 25) as to contribute a negligible amount to the variation concerned. In these circumstances, however, the species will have had little experience of it and there will have been but small opportunity for dominance-modification (*Butterflies*, pages 257-262) to take place. Therefore the heterozygote will often be semi-dominant only. Certainly it will not be recessive: were it so, it would not be an agent in producing polymorphism. An important consequence follows from this. It is known that one of the commonest types of mutation in all organisms is the recessive lethal or semi-lethal: one therefore which produces a gene which kills or incapacitates the individual when homozygous but is innocuous when heterozygous. Naturally these genes are eliminated by selection on the one hand, and maintained by mutation on the other. But such lethals can accumulate in that part of a chromosome which is close to a dominant or semi-dominant gene controlling a polymorphism, since this will to a predominant extent be present in the heterozygous state. Here the lethals will be sheltered from selection even though as heterozygotes they will be quite frequent. They will only be eliminated in the rare homozygous condition of the 'switch-gene' responsible for the polymorphism, or as the result of crossing-over transferring them to the other chromosome containing its recessive phase. But they will seldom thus be separated from the dominant which protects them if situated close to it, for the chance of a cross-over taking place in a short length of chromosome is small. The result is that the homozygous dominant phase of a polymorphism will usually become less hardy than the heterozygous one; and if the latter be at an advantage, as it usually must be in order to have spread through the population at all, this tends automatically to reinforce the polymorphism. This accounts for the singular fact that even when there is a clear ecological reason for maintaining diversity in a population, as in mimicry (pages 102-7), the homozygous dominants tend to become disadvantageous.

Polymorphism in British Moths

The control of balanced polymorphism, and the conclusions reached in the foregoing account, can now be illustrated by examples chosen from British moths, (see also Ford, 1953b).

Few polymorphisms have been studied so thoroughly as that of the Scarlet Tiger, *Panaxia dominula* L. Hypsidae, in one of its colonies near Oxford. In this locality a variety *medionigra* (Plate 11, figures 3 to 5), of great rarity elsewhere, is in some seasons evidently at a marked advantage. It is, as already explained (page 21), a heterozygote which resembles the normal homozygous *dominula* (figure 1) more closely than the rare one *bimacula* (figure 2). The situation will be discussed in detail from the ecological and evolutionary points of view in Chapter 14. Here it is only necessary to note those features which illustrate polymorphism as such. *Medionigra* has been at a selective disadvantage of about 10 per cent compared with *dominula* since 1941, previous to which it had for a number of years been favoured by selection. Consequently the frequencies of the forms have varied in different generations (the species has but one brood in the year). The circumstances chiefly responsible for the spread of this gene must have been some ecological condition in the very exceptional type of marsh which constitutes this particular locality. However, if the viability of all three genotypes were equal, polymorphism would still be maintained, owing to the unusual situation discovered by P. M. Sheppard, that the gene concerned influences the mating preference of the females, which prefer to pair with males of a different genotype from their own.* Since *medionigra* occupies the status of a rare mutant except, as far as is known, in this one locality, it must ordinarily be sufficiently disadvantageous to counterbalance the tendency of normal specimens to mate with it rather than with their own form. The homozygous mutants, *bimacula*, are certainly feeble compared with the heterozygotes. It seems, however, that the disadvantageous recessives which they have evidently accumulated operate against the imagines rather than the early stages; for, though lethargic and disinclined to fly, their frequency in the wild population does not differ detectably from that expected on the assumption that the three genotypes are equally healthy.

The Riband Wave, *Sterrha aversata* L., is an abundant dimorphic species. There is a common plain form *remutata* (Plate 13, figure 1) and a much rarer one in which the wings are crossed by a broad dark band, *aversata* (figure 2). Perhaps about 5 per cent of the population consists of this phase, and there is no part of the country where it seems to be especially frequent. It is normally a heterozygote which is nearly dominant, for when homozygous banded insects are bred in the laboratory they prove to be only slightly more extreme. I have reared this species myself and found the number of homozygous barred examples fell slightly below expectation in segregating families but to an extent which was not significant, though it might well become so if larger totals were raised.

The polymorphism of the Mottled Beauty, *Cleora repandata* L.,

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*This applies to both homozygotes and to the heterozygote.

Selidosemidae, is, on the other hand, related to the geographical distribution of the species, which is uniform in Eastern Britain where the normal unbanded *repandata* alone is found, but dimorphic in the West. This includes both the extreme south and north of the country: North-west Scotland, and the Devon-Cornwall peninsula. In that region a beautiful black-banded form *conversaria* occurs in addition. This is an incomplete dominant, the ground-colour of the heterozygotes being grey or brown and of the homozygotes white. There is evidence that the homozygotes are unduly rare in some segregating families, but not in others. This is not unexpected, depending on what disadvantageous recessives have accumulated near the locus of the *conversaria* gene, and on the rest of the genetic constitution of the individuals. Cockayne fortunately made a large count of wild specimens in Ross (North-west Scotland) with the following result: 480 *repandata*, 141 heterozygous and 5 homozygous *conversaria*. We have very few such estimates of the frequency of polymorphic forms in nature, though they are badly needed. They would indicate the extent to which the proportions vary with locality, and possibly the conditions controlling such variation; also, when the heterozygotes and ‘ dominant ’ homozygotes are distinguishable, whether the latter group is deficient and to what extent, and whether or not it always is so. Here is a subject on which collectors could secure valuable information.

The fact that the Mottled Beauty is dimorphic in one part only of its range in this country suggests the possibility that other species purely monomorphic here may be affected by polymorphism elsewhere. There are in fact a number of instances of the kind, but it will suffice to mention one of them. The Barred Red, *Ellopia prosapiaria* L., Selidosemidae, has two phases in Central Europe; one, the commoner, is reddish-brown and the other, *prasinaria* is greenish. The latter is a simple recessive. Only the brown form reaches Britain, save that specimens of *prasinaria* have on a few occasions been found as an extremely scarce variety, certainly not as a dimorphic phase.

The Orange Moth, *Angerona prunaria* L., Selidosemidae, appears to be a dimorphic species throughout its range. There is a common unbanded form *prunaria*, and a rarer one, *corylaria*, with the orange brown colour of the male, or the yellow of the female, restricted to the central area of the wings by dark pigment. This is almost a complete dominant, but the homozygotes are identifiable owing to the absence of the small dark lines in the pale areas. There is no evidence on the relative viability of the three genotypes, and information on the point would be welcome. However, the width of the band in *corylaria* is subject to considerable genetic variation depending upon segregation occurring in the rest of the gene-complex. Such variation is therefore susceptible to the effect of selection, as Douglas Smart has demonstrated experimentally in this insect. By choosing more or less banded parents respectively, he has on the one hand been able to reduce the band to a small spot in the centre of the fore-wings and on the other greatly to extend it. He is to be congratulated upon this result. It demonstrates an important feature of polymorphism: that the characteristics of the different phases can be modified in the course of evolution while yet remaining under the control of a single major gene or genes which act as a switch in determining alternative forms. Moreover, since even the rarer phases of a polymorphism are very abundant compared with unifactorial varieties maintained by recurrent mutation, the opportunities which they offer for selective adjustment are far greater. Consequently minor evolutionary changes can take place much more rapidly under polymorphism than in other circumstances.

Two forms of the Dark-barred Twin-spot Carpet, *Xanthorhoe ferrugata* Cl., Hydriomenidae, are found together throughout the range of this common moth in Britain. The bands on the fore-wings are black or dark purplish in the more frequent, red in the rarer. The latter is a simple dominant but occasional intermediate specimens are found. Such variation is probably genetic, of the same type as that affecting the *corylaria* form of the Orange Moth. Red-banded specimens of *X. ferrugata* are relatively more frequent in some parts of the country than in others and estimates of them in different places are very desirable. It would be of much interest to determine if the homozygous dominants are at a detectable disadvantage in those localities where the heterozygotes are frequent.

The interesting dimorphism of the Wood Tiger, *Parasemia plantaginis* L., Arctiidae, has already been mentioned as providing instances of sex-controlled inheritance. It is strictly related to the geographical distribution of the species. The form of the male with a white ground colour, *hospita*, is entirely restricted to mountains and high latitudes. In such places the gene responsible for it must have some advantage which it does not possess at lower elevations. It would be of great interest to study the survival of the two types in a series of temperature-experiments. The frequency of *hospita* varies from one to another of its localities. In the English Lake District it has been assessed as up to 5 per cent of the males, but no proper counts have been made and this is a most unreliable estimate. Schulte has recently reported that all the males are of the *hospita* form in a locality near Abisko in Swedish Lapland. The red-marked females of the Wood Tiger, probably sex-controlled dominants, are, as far as Britain is concerned, almost restricted to North Wales, Westmorland and the Aberdeenshire coast, where that form is not uncommon in the female population. Here too the advantage of the gene concerned is evidently related to special features of the ecology of the insect. Considerable information on this situation might be obtained by studying its genetics in carefully controlled environments.

Dr. H. B. D. Kettlewell finds that a dark form of the larva of the Scarlet Tiger is, at least in some colonies, sufficiently frequent to constitute a dimorphism. Its genetics are as yet uncertain and it is not even known if it is controlled by a single gene. However, its occurrence indicates that a search for polymorphism among the complex and varying patterns of larvae is likely to be rewarding. Dr. E. A. Cockayne has pointed out to me that though the larva of the Pale Eggar, *Trichiura crataegi* L., Lasiocampidae, is very variable, one form, black with orange rings, is strikingly distinct. It occupies a high proportion of the larval population in some localities and a low one in others, and is likely to represent a dimorphism which must be under simple genetic control.

No information exists on the polymorphism of a number of species of British moths, while in other instances our knowledge of it is vague and unreliable. Here are excellent opportunities for research of a kind which could well be carried out by collectors accustomed to breeding insects. Some of the features to which special attention should be paid in the course of such work will now be apparent.

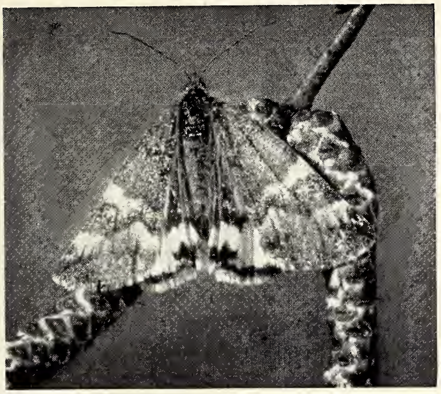
In addition, brief reference should be made to two dimorphic species both of which present features of interest and of technical difficulty. The Dingy Footman, *Eilema griseola* Hb. (Plate 13, figure 3), Arctiidae, is usually of a light greyish shade, but there exists a straw-coloured form *flava* (figure 4) so different as at one time to have been thought a distinct species. This phase represents the converse of a condition already mentioned, for though the insect is widespread in Europe it is said to be dimorphic only in Britain: the pale form being, apparently, unknown elsewhere. Probably *flava* is a single dominant or semi-dominant but, feeding on lichen, the species does not seem easy to breed. The sexual dimorphism of the normal form of the Silver Cloud, *Xylomyges conspicillaris* L., Caradrinidae (Plate 13, figure 8 male, figure 9 female), which occupies a considerable proportion of the population in Worcestershire, is largely obliterated in the dark alternative phase *melaleuca* (figure 10 male, figure 11 female) found predominantly in Devon and Cornwall. The moth is almost confined to these two areas in Britain and is difficult to obtain.

The species so far mentioned are dimorphic only, and the fact that in a few of them the heterozygotes are distinct, hardly constitutes a trimorphism, since one of the homozygotes then takes the status merely of a rare variety. However, we have some information on the genetics of moths having multiple phases. In sub-tropical and tropical mimetic butterflies these are often determined by several interacting genes, often with sex-controlled inheritance. The two distinct dimorphisms of the European, though not British, Burnet Moth *Zygaena ephialtes* L. have been discussed in relation to genetic interactions. A more complex instance is provided by the Common Marbled Carpet, *Dysstroma truncata* Hufn., Hydriomenidae. Many aberrations of this insect are known. Some are the result of continuous variation, others seem to be rare varieties probably maintained only by mutation-pressure, but others again are polymorphic forms. The dark variety *nigerrimata* (Plate 13, figure 14) is a semi-dominant (N –), the heterozygotes being the less extreme. The grey *perfumata* (figure 13) is frequent in its heterozygous phase (P –) but the homozygotes, which constitute the dark-banded *albonigrata*, are rare. A common form *rufescens* (R –), with an orange central area to the fore-wings (figure 12), is almost completely dominant, and K. Groth demonstrated that the homozygotes fall significantly below their expected frequencies in segregating families and are less fertile than normal. *Russata* is the triple recessive (nnpprr). These three genes apparently assort independently, but the data do not exclude the possibility of at least loose linkage between them.

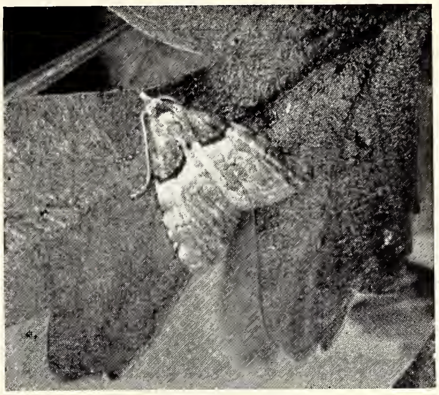
A striking polymorphism badly in need of investigation is that of the Jersey Tiger, *Euplagia quadripunctaria* Poda, Hypsidae. This is a conspicuous insect often active by day. It is allied to the Scarlet Tiger, the fore-wings being whitish with longitudinal chocolate markings and spots. The hind-wings are spotted with black, and their ground-colour may be scarlet, various shades of terra-cotta, or clear yellow. Unfortunately, though this insect has often been raised from the egg it is extremely difficult to pair in captivity, a circumstance which has so far prevented the study of this striking colour-series. It seems likely that the difference between the specimens with yellow hind-wings is unifactorial compared with the red and terra-cotta phases and probably recessive to them. The genetics of these latter, however, are apparently not simple, and it would be an intriguing task to elucidate them. The numbers of the three groups in nature make it clear that the terra-cotta, orange and salmon coloured individuals are not heterozygotes between the red and yellow, which a casual inspection might well suggest. Probably the distinction between them and the red form is controlled by one or more genes which do not act in the genotype giving rise to the yellow phase, while a combination of genetic interaction and environmental modification is a possible interpretation of this colour-series. This species is restricted to a small strip of coast in South Devon. It only reached England in the middle of last century, having migrated or been brought from the Channel Islands.

On reviewing these examples of balanced polymorphism in British moths it will be evident that among them they illustrate the general features of this condition that have already been outlined. Also that they provide a fascinating field for investigation. It is true that information of importance is to be obtained by breeding some of the forms at constant temperatures, and in constant environments in other respects. That aspect of the work can be left to those who have the use of laboratory equipment. Even so, much remains to be done of a kind which can be undertaken by moth collectors as an extension of their hobby, particularly in relation to the ecology of polymorphic phases, their relative viability, and the interaction of the genes controlling them.

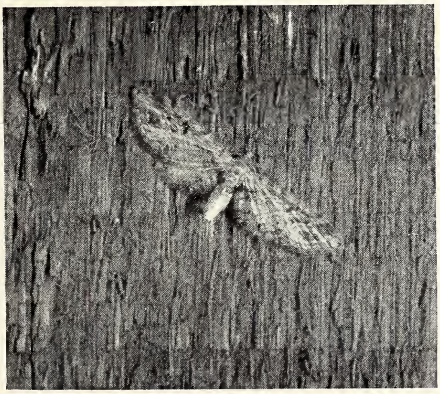
Finally, some evolutionary aspects of polymorphism must briefly be mentioned (for further information on them, see Sheppard 1953). It has already been pointed out (page 64) that the balanced type must arise when the heterozygotes are at an advantage compared with either homozygote. This is not an infrequent situation, for genes probably always have multiple effects (page 49), while it is much easier to damage than to improve a complex system such as the body of an



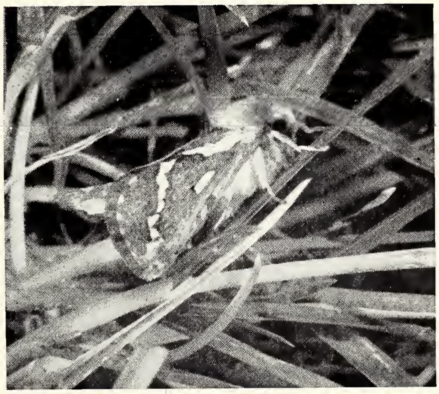
1. Orange Underwing, *Brephos parthenias* (X 1.5)



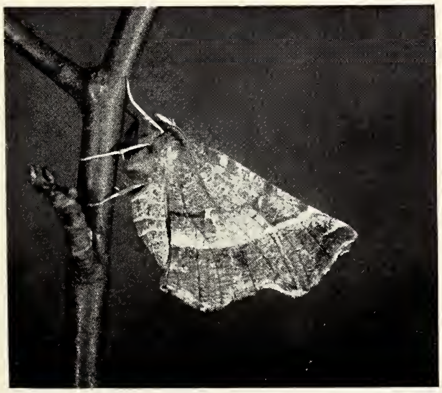
2. Short-cloaked Moth, *Nola cucullatella* (X 2)



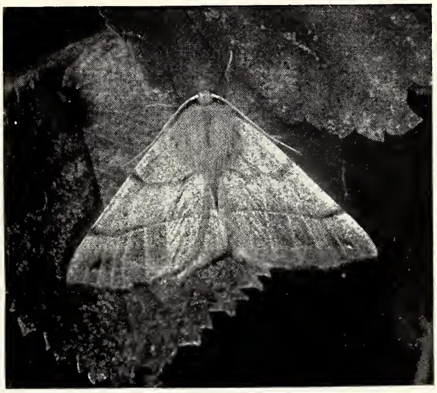
3. Mottled Pug, *Eupithecia exiguata* (X 1.5)



4. Common Swift, *Hepialus lupulinus* (X 2)



5. Early Thorn, *Selenia bilunaria* (X 1.5)



6. Feathered Thorn, *Colotois pennaria* (X 1.5)

Plate VII. PROTECTIVE SHAPES AND PATTERNS

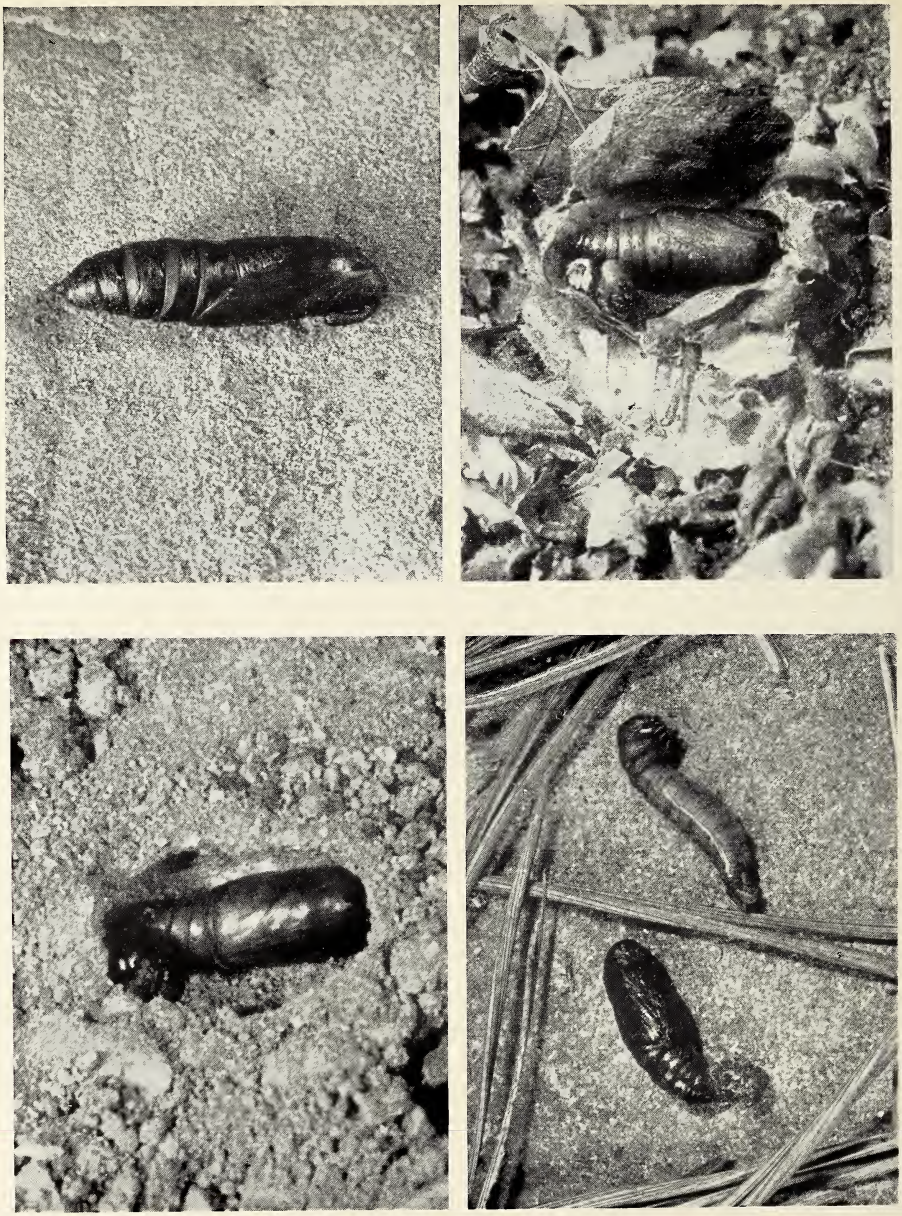


Plate VIII. PUPAE

1 (*top left*). Privet Hawk, *Sphinx ligustri* (X 1); 2 (*top right*). Yellow Horned, *Achlya flavicornis* (X 2); 3 (*lower left*). Merveille du jour, *Griposia aprilina* (X 2); 4 (*lower right*). Bordered White, *Bupalus piniarius* (X 1. 5)

animal. Therefore, if one of them be useful the others will probably be harmful. Now selection will tend to make the advantageous effects of a gene dominant and the disadvantageous ones recessive (*Butterflies*, pages 257-62). The heterozygotes will then possess only advantageous characters, since in them the dominants are manifested and the recessives obscured, while the two homozygotes will have some that are advantageous and others that are disadvantageous. Consequently, selection will favour the heterozygotes and lead to polymorphism.

It is desirable for those genes which have beneficial effects to be associated. Therefore selection will tend to increase the linkage between them if they are on the same chromosome, for the frequency of crossing-over is under genetic control. If, on the other hand, they are on different chromosomes, any translocation which brings them on to the same one will be favoured. These considerations account for the fact that many polymorphisms are controlled by systems of closely linked genes. A search for such linkage, so widespread in other organisms, should be a high priority in studying the genetics of the Lepidoptera.

CHAPTER 6

DISPERSAL

Minor Ecological Barriers

THERE ARE TWO DISTINCT aspects of dispersal: the spread of individuals, enabling them to colonise new territory, and the spread of genes. It is clear that the methods by which a species can extend its range are capable also of interchanging genetic material between its different populations, whether or not their relative densities are altered in the process. On the other hand, the scattering of genes may be achieved by means which cannot increase the distribution of the organism as, for instance, by flight in those moths in which the males are winged and the females wingless. It will be convenient to discuss these two types of dispersal separately.

We are at present extremely ignorant of the extent to which minor ecological barriers check the free movement of individuals and so tend to break up apparently continuous populations into small isolated or semi-isolated units. I believe that the sub-division of distinct types of habitat such as woods, moorland, fens or meadows, into disconnected areas is, in many species, a more important isolating agency than has been realised, even when the insects concerned can fly across the intervening ground in a few minutes. I would go further, and suggest that the presence of hedges tends to a considerable degree to circumscribe some moths and butterflies within individual fields, even though they could pass from one to another with the greatest ease. The Meadow Brown Butterfly and the Grass Rivulet Moth could cross an ordinary hawthorn hedge, flying a little above their normal height to do so, in a few seconds; but it is probable that such apparently trivial obstacles nevertheless constitute effective partial barriers to them.

This matter is of importance since evolution proceeds faster in a community that is broken up into small isolated or semi-isolated populations than in a continuous one (see Chapter 14). Moreover, the subject is admirably suited to amateur investigation by the marking of specimens. This can easily be done in butterflies and moths by means of cellulose paint (see *Butterflies*, pages 271-2). Unfortunately, though the more spectacular but less fundamental subject of migration has attracted much attention, data upon the effects of minor ecological barriers are almost lacking. Perhaps the only information of the kind available in the Lepidoptera is supplied by the quantitative studies of the Meadow Brown carried out by W. H. Dowdeswell and myself on the uninhabited island of Tean, Isles of Scilly. This is approximately half a mile in length and contains three areas of long grass, bracken and bramble which are inhabited by this insect. These are separated from one another by two strips of short, almost lawn-like, turf, about 210 and 130 yards long respectively, that are unsuited to it. The species is an active one, powerful on the wing, and it frequently covers considerable distances. It could certainly pass from one to another of its habitats on Tean in a few minutes, yet it hardly ever does so whatever the direction of the wind may be.

We estimated the sizes of the three colonies in 1946 by the method of marking, release and recapture (Chapter 14) and found them to be very unequal, consisting respectively of about 500, 3,000, and rather over 15,000 specimens. The butterflies flew freely even in dull weather, but only once did we see one crossing either of the intervening regions of short grass, though we were walking over them many times a day for nearly three weeks. Moreover, out of 183 marked specimens recaught during that period, only three had originally been taken in a different area (Dowdeswell, Fisher and Ford, 1949). It was clear therefore that the strips of short grass proved an effective barrier to this species and we have recently found that one of the three colonies is acquiring characteristics recognisably distinct from the others as a result of the isolation which they provide (Dowdeswell and Ford, 1953). Moreover, the population of the Meadow Brown on the islands of Tean and St. Helens are quite distinct, as indicated by the distribution of spotting in the females (see Chapter 14). Yet they are only 440 yards apart, a distance which this insect can fly quickly and easily.

It is to be hoped that such ecological studies will now be carried out in a wide range of animals, including moths. They will probably show that these small ecological barriers are much more important in isolating populations, and therefore in promoting their rapid evolution, than has been suspected.

1
Male
CUMBERLAND

2
Female
CUMBERLAND

3
Male
SUSSEX

4
Female
SUSSEX

5
ARGYLL

6
KENT

7
KINCARDINE

8
CUMBERLAND

9
SURREY

1-4. Common Heath, *Ematurga atomaria:* 1 & 2 typical, 3 & 4 recessive variety; 5-7. Garden Tiger, *Arctia caja:* 5 typical, 6 yellow, 7 streaked variety; Hebrew Character, *Orthosia gothica:* 8 typical, 9 var. *circumsignata.*

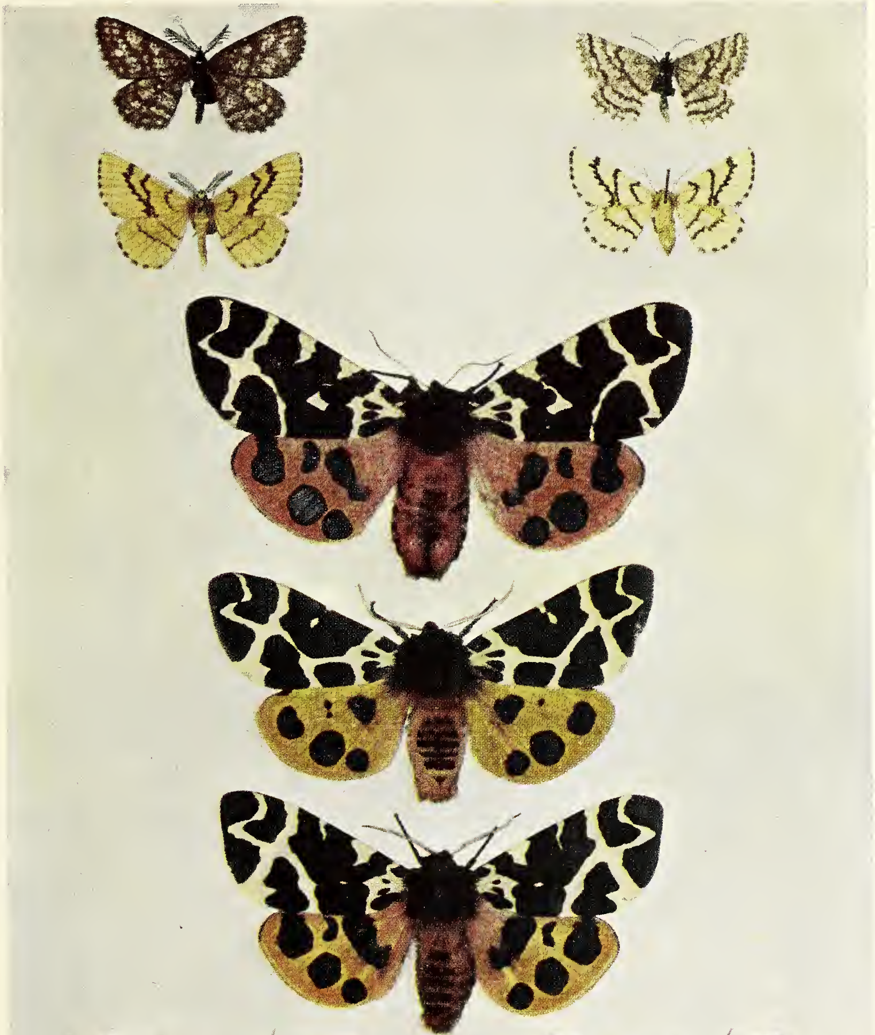


Plate 9

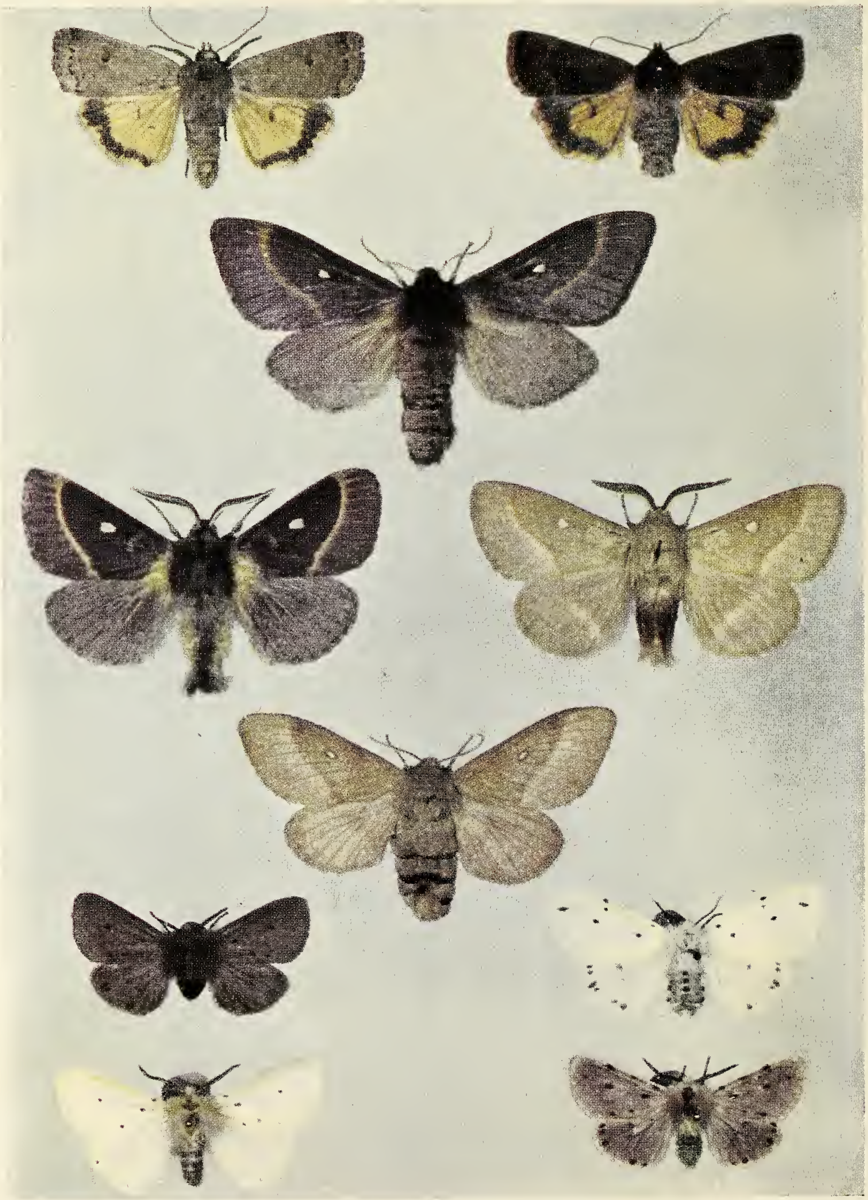


Plate 10

1
CUMBERLAND

2
ORKNEY

3
Female
CORNWALL

4
Male
CORNWALL

5
Male
DUNGENESS,
KENT

6
Female
DUNGENESS,
KENT

7
Male
BERKSHIRE

8
Female
BUCKINGHAMSHIRE

9
Male
CORK

10
Male
CORK

---

1 & 2. Lesser Yellow Underwing, *Triphaena comes:* 1 typical, 2 var. *curtisii;* 3-6. Grass Eggar, *Lasiocampa trifolii;* 7-10. Muslin, *Cycnia mendica:* 7 & 8 typical, 9 & 10 var. *rustica*

Dispersal of Individuals

Evidently flight is the chief agent in dispersing moths. It allows a free interchange of genes within small colonies, and at least some degree of gene-flow between discontinuous groups, though to an extent which depends very much upon the species. When, as usual, both sexes can fly, it is sometimes possible for these insects to invade new habitats, such as a recently planted wood, rather quickly; also to repopulate old ones after the severe reductions in numbers to which many of the Lepidoptera are periodically exposed. At their minimum density they tend to become restricted to those localities which are the most favourable for them, from which they later spread when their numbers rise. The artificial transport of specimens in their early stages and the crawling of the caterpillars are also quite effective means of dispersal. Indeed, those species with wingless females are almost entirely dependent upon such agencies. These include the Winter Moth, *Operophtera brumata*, L., Hydriomenidae (Plate 5, figure 3 the female, 4 the male), and members of *Erannis* and related genera of the Selidosemidae (for instance, the Mottled Umber, *E. defoliaria* Cl., Plate XVIII, figure 1 the male, 2 the female). Their rather spider-like females can walk up and down a tree-trunk, but to this their movements are approximately confined. The degeneration of the female Vapourer, *Orgyia antiqua* L., Lymantriidae (Plate 1, figure 1) is more extreme. She clings throughout her life to the cocoon from which she emerged, yet the moth is to be found commonly throughout Britain and Ireland, feeding upon a great variety of trees and bushes. Dr. Kettlewell tells me that the conversion of the female into a mere egg-laying machine is carried still farther in a South African species, *Bracharoa dregei* H.S., which belongs to an allied genus, for here she never even makes her way out of the cocoon. The male plunges into it in order to pair with her, and her eggs are therefore of necessity laid inside it also. The young larvae make their first meal by devouring their living mother; one would have thought that so economical a practice would have been more widely adopted.

It is remarkable that many of the moths with flightless or even motionless females are very widely distributed. To-day, doubtless, the eggs or larvae are to a slight extent carried by human agency, but they certainly do not owe their extensive range to that circumstance. This must have been achieved long ago (Chapter 11), principally by the crawling of the larvae from one suitable habitat to another. They may also swing from place to place as they dangle at the end of a silken thread. In addition, it has been stated that the winged males fly short distances with the wingless females during copulation. The relative sizes of most of them would seem to make this very difficult and the evidence for it is not decisive. However, it is possible for copulating males to fly carrying the inert female with them in certain species in which both sexes are winged.

Many moths powerful on the wing are yet extremely localised and rarely leave their favoured haunts. The Scarlet Tiger, *Panaxia dominula* L., Hypsidae (Plate 15), which forms circumscribed colonies along river-banks and in marshes, provides an example of them. Others, with a wide range of environmental tolerance, wander to some degree as, apparently, does the Peppered Moth, *Biston betularia* L., Selidosemidae (Plate XXIII). Others again are migratory.

Migration

The status of those species which maintain themselves in these islands wholly or partly by migration can best be indicated by specific instances. These are chosen as illustrative examples only: it is not intended that they should form a comprehensive list of our migrant Lepidoptera and indeed they represent but a small proportion of them.

Certain resident British moths are augmented by migrants from the Continent, the influx of which makes them widespread and common in some seasons while in others their distribution is restricted to their endemic range. Thus the Pearly Underwing, *Peridroma saucia* Hb., Caradrinidae (Plate XX, figure 11), seems to be permanently established along the south coast, but its more general occurrence from time to time is due to the arrival of immigrants. The Dark Sword Grass, *Agrotis ypsilon* Rott., Caradrinidae (Plate XX, figure 10), though on the whole a commoner species here, seems to be rather more dependent upon the arrival of specimens from abroad. However, considerable numbers of the imagines, which emerge in the late summer, hibernate successfully and lay eggs in the spring.

Some moths with a clearly defined British range are occasionally found in distant parts of the country, often as single specimens only. These may be individuals which have wandered far beyond their normal confines, but in some instances they are dissimilar to the native race and are immigrants from abroad. Thus, the Great Brocade, *Eurois occulta* L., Caradrinidae, is a resident in Scotland, but now and then examples are found in southern England. These are much paler than the indigenous form and have reached this country from Belgium and Scandinavia (Plate xx, figure 1 Scotland, figure 2 Essex). A further instance is provided by the Speckled Footman, *Coscinia cribraria* L., Arctiidae, which is an exceedingly local species found only on heaths in Dorset and the New Forest. Our race is white, freely speckled with black dots (Plate xx, figure 4). On very rare occasions a different and nearly immaculate form (figure 3) has been taken elsewhere in the south of England, and such individuals are immigrants.

A certain number of moths, as of butterflies (see the previous volume, page 154), constantly found in Britain are maintained entirely, or to an overwhelming extent, by immigration, so much so that, were this to cease, they would almost, or completely, disappear from these islands. Perhaps the commonest of them is the familiar Silver-Y, *Plusia gamma* L., Plusiidae (Plate 16, figure 4), which reaches us in the spring from southern Europe. The specimens which arrive at that time breed here and in some seasons populate Britain with myriads of the moth in late summer.

One of the most noteworthy of this group of migrants is the Humming-bird Hawk, *Macroglossa stellatarum* L., Sphingidae (Plate 3, figure 3), which in many seasons is a common insect in England. It is possible that a few specimens hibernate successfully with us, but its existence in Britain depends upon migration from Southern France in the spring. This is a day-flying moth, exceedingly swift upon the wing and provided with a long proboscis, shown uncoiled in the figure, with which it probes flowers, hovering before them with wings vibrating so rapidly that they are to be seen only as a haze on either side of the body. Their movement produces a hum so high-pitched that, though it can be heard by most women, the majority of men become deaf to it; for the pitch audible to them drops when the voice breaks during adolescence. The darting movement, the hovering before flowers, the general size and appearance, and the high-pitched hum, cause this moth to resemble the humming-birds of the New World to a remarkable degree. Indeed when first I saw a Humming-bird in the United States I was for a moment deceived, thinking it a moth of the genus *Macroglossa* with which I was so familiar in Europe.

The status here of the Convolvulus Hawk, *Herse convolvuli* L., Sphingidae (Plate xx, figure 5), is similar, except that it is much less common. However, it is not infrequently to be found at dusk hovering in front of petunias or the flowers of the tobacco plant, which its immense proboscis, three times the length of its body, enables it to probe. Judged by wing-expanse, though not by size of body, this is the largest British moth. Larvae have seldom been found in this country. Two forms of them are known: bright green or blackish (page 58-9). It is safe to say, however, that nearly all the imagines seen here have flown from the neighbourhood of the Mediterranean, a distance which this powerful insect can easily traverse. Indeed at times it has reached the north of Scotland.

A further example of a species which maintains itself not uncommonly in Britain purely by migration is provided by the Gem, *Nycterosea obstipata* F., Hydriomenidae. It is illustrated on Plate xx, figure 6 the male and 7 the female, from which it will be seen that this is a sexually dimorphic insect. Immigrants arrive in the spring and produce several generations during the summer: the larvae feed on groundsel and various common plants, but the Gem seems unable to survive the winter here.

The moths just mentioned are regular visitors, but there are many which reach these islands only on rare occasions. Some, like *Cosymbia pupillaria*, Sterrhidae (Plate 29, figure 2), have been found only two or three times, others but once. These may represent unusual acts of migration, chance importations with plants or, like the Monarch Butterfly (*Butterflies*, page 158), they may have come as passengers in the hold of a ship. Such exceptional occurrences are not of special interest. However, numerous species have made occasional appearances here over a long period of time and these are most likely to be rare migrants, for many of them have been taken in numbers at least once during the last 150 years, which would be unlikely were they casual importations with plants. This may either mean that an exceptional migratory swarm had arrived, or that climatic conditions had allowed the offspring of a small number of immigrants to feed up successfully and produce a large British-born generation later in the same year.

The Crimson Speckled, *Utetheisa pulchella* L., Arctiidae (Plate 3, figure 9), does not seem to be established as a resident north of the Mediterranean coast. It has a very wide range and is a notable migrant, occasionally wandering as far afield as Britain. One or two specimens have been recorded here every few years since early last century. In favourable seasons, eggs laid by immigrant females have produced a subsequent brood. However, the larvae will feed only in the sunshine, a habit with makes it impossible for this insect to establish itself permanently in Britain.

The Scarce Bordered Straw, *Heliothis armigera* Hb., Caradrinidae (Plate xx, figure 9), is one of the most widely distributed moths in the world, occurring apparently in all but the Arctic and Antarctic regions. I have myself seen it in Australia. Occasional specimens have been reported from many parts of Southern England, and a few from Ireland, since 1840; while the larvae have once or twice been found wild and in imported fruit. However, it may be an established resident, though probably on a temporary basis only, in the neighbourhood of Torquay. In the United States this is a serious pest of corn and other crops, including cotton and tomatoes.

The American Wainscot, *Leucania unipuncta* Haw., Caradrinidae (Plate 3, figure 8), is also an almost worldwide species, but rare in Europe though found in Madeira. In the United States, where it is known as the ' Army Worm,' this is a very destructive insect. About two dozen have been taken in England since the beginning of the last century. Like that previously mentioned, it is an inhabitant of warmer countries than Britain, though it may occasionally breed in South Devon.

The Delicate, *Leucania vitellina* Hb., Caradrinidae (Plate xx, figure 8), is a Southern European moth which is occasionally found in England. Specimens obtained in the South-eastern Counties are pale in colour and sporadic in occurrence, and they are certainly migrants. Those found in the South-west are darker and it is probable that they breed there.

Plusia ni Hb., Plusiidae (Plate 3, figure 7), much resembles a small and pale specimen of the Silver-Y (page 80), but the silver mark on the fore-wings, instead of being formed like a Y as in the latter species, is made up of a U with a dot, generally detached, below it. The species is apparently very rare but must often be confused with the Silver-Y on the wing, and its larva has occasionally been found in this country. In 1952 the imagines were taken in some numbers in Southern England. It probably migrates to us from the northern shores of the Mediterranean, and in Italy I once found that about twenty per cent of the population of what appeared to be the Silver-Y was really this species.

Several of the more magnificent Hawk Moths are known only as rare migrants here. That shown on Plate 3, figure 6 is the Striped Hawk, *Celerio livornica* Esp. It has a wide range in the sub-tropics and tropics, I have myself seen it at Singapore, and it is probably a resident as far north as the European coast of the Mediterranean. It is a great wanderer and specimens are recorded in Britain in most years, while on a few occasions large numbers have been reported, as in 1950. The larva has occasionally been found feeding upon Fuchsia and other plants.

The migration of the Vestal, *Rhodometra sacraria* L., Hydriomenidae (Plate 3, figure 4), has thrown new light upon its genetics. This insect is resident in Southern Europe, North Africa and elsewhere, and migrant specimens have occasionally been recorded in Britain for about the last hundred years. Rarely had more than one or two been seen in a season, but in 1947 a large number arrived and bred here. Later in the year the species actually became common in stubble fields, where the larva fed on Knot-grass, *Persicaria.* Normally the fore-wings of this moth are pale yellow with a thin oblique red stripe. However, the English specimens showed a wide range of variation, often being suffused with red or grey, and the stripe varying to brown and blackish. These forms were known previously, but only as extreme rarities. Dr. Kettlewell, who investigated the matter, finds that certain genes responsible for controlling pigmentation take effect only at low temperatures. Consequently the colour of this moth rarely varies in the warm climate of its normal habitat, but does so here.

There are a number of occasions on which migrants have reached this country and have successfully founded a colony of a species previously unknown here or of sporadic occurrence only. Such populations are not usually permanent, but may last for a period of years until obliterated by an exceptionally inclement season. If, on the other hand, they chance to be established at a time when our Lepidoptera are on the average increasing in numbers and extending their range, consequent upon long-term fluctuations in climate (Chapter 14), it is possible that they may prove very successful, though this does not necessarily mean that they have been completely incorporated into our fauna, for they may not be able to survive the time when the conditions become less favourable.

Several instances in which migrants have established themselves temporarily in Britain are discussed in Chapter 10; see also the account of *Sedina buettneri* (pages 123-4), and of *Trigonophora flammea* (page 228). Therefore it will now suffice to give three examples representing different stages, or degrees of success, in the colonising of this country by a moth previously unknown or of great rarity here.

Until recently it was thought that only three authentic British specimens of the Varied Coronet, *Hadena compta* Schiff., Caradrinidae, were in existence. Yet in 1948 eleven were caught in a garden at Dover and since that time the moth has proved to be locally common there, the larvae being abundant on Sweet William plants, and it is now spreading in the neighbourhood. This, like the Clifden Nonpareil (page 147), is one of the species whose range has in recent years extended northwards in Europe.

Up to twenty years ago only about half a dozen specimens of the White-L Wainscot, *Leucania l-album* L., Caradinidae (Plate 3, figure 1), had been recorded in Britain. However, in 1933 several were taken at the Lizard lighthouse, and two years later the moth was found in numbers in South Devon. It has now spread along the coast to the Isle of Wight and is certainly well established for the time being. There can be no doubt that this is an instance in which a migrant species has founded an extensive population in this country.

The most successful recent colonist among the moths of these islands is the Golden Plusia, *Polychrisia moneta* F., Plusiidae. The first British specimen was caught in 1890. Since that date the species has spread throughout England, becoming common and well established in the South, and it has now reached Southern Scotland. The larva feeds upon Monkshood, *Aconitum*, and Larkspur, *Delphinium*, and to-day it is generally to be found wherever these plants are grown in the southern counties.

Migrant Lepidoptera may arrive in this country anywhere along the south coast, and some Scandinavian species, like the Camberwell Beauty Butterfly (*Butterflies*, page 155) and, I think, the Great Brocade (page 80), occasionally reach those counties bordering the North Sea. It seems, however, that there are certain migration-routes along which a disproportionately large number of moths travel. Unfortunately, the evidence bearing on this subject is unsatisfactory, owing to the unequal nature of the observations involved, depending partly upon the availability of entomologists and upon the presence of suitably placed lighthouses, at which the specimens are often collected. Yet there appears to be some indication that migrants tend especially to arrive in the Folkestone area, the Isle of Wight, at Portland, Torbay, in the Falmouth district and at the Lizard. In some respects butterflies provide better proof of such migration-routes than do moths. The influx of Bath Whites to Falmouth in 1945 illustrates this point. In that year this rare wanderer to our shores became almost common in Southern England, but it was most unequally distributed along the coast and was actually abundant at Falmouth. Some of these migration-routes can be traced inland across the country; for example to the north coasts of Devon and Cornwall where in the deep narrow valleys at the mouth of certain streams the insects pause in their onward flight and accumulate.

I believe that the migration of Lepidoptera to Ireland has been much under-estimated. The migrants may arrive direct from the Continent, passing west of the British mainland, or they may cross south-western England on the way. Very little collecting has been done in Ireland; yet there is strong evidence of the repeated capture there of migratory species from the Mediterranean region. A few instances will suffice to establish this. Several individuals of the Crimson Speckled (pages 81-2) have at intervals been taken widely scattered about the southern half of Ireland. In October 1936 the third British specimen of the Bloxworth Snout, *Hypena obsitalis* Hb., Plusiidae, a southern European and North African species, was obtained on ivy blossom at Ummera, Co. Cork, together with eleven examples of the Gem which, as already explained, is a well-known migrant. In 1931 eleven *Plusia ni* (page 82) were caught at the same place, where also fifty-eight American Wainscots had been obtained in 1928. This latter record has, however, no bearing on the matter in hand, for ships arrive in Cork Harbour from the United States and these insects were probably the offspring of one or more specimens carried on them. Yet their occurrence demonstrates the possibility that species from the New World may become established in Ireland. The record of *Plusia variabilis* Piller from Castle Kevin, Wicklow, in August 1887 appears to be genuine. There are old reports of it from the Salisbury district, but this is purely a southern European species. Many other undoubted instances of migration from Europe to Ireland might be quoted. They demonstrate the great potentiality for colonising distant lands possessed by certain of the Lepidoptera.

The advantage to the species of large-scale migration must consist both in the opportunities it provides for the scattering of genes and for colonising new territory. The latter is an important consideration, since at no time are the conditions of the countryside static. Consequently, habitats may become available in distant places which had not been suitable in the past.

It is fairly certain that migration is hardly ever undertaken to relieve local over-crowding, for it is seldom that a moth becomes so abundant as to destroy its food-supply. *Tortrix viridana* and the Mottled Umber, *Erannis defoliaria* (page 116), may do so in English oak-woods, but this does not lead them to migrate; while the requisite food-plants often remain abundant in the region whence migrant species set out upon their long journey.

There has been much speculation concerning the conditions which produce migration. Such stimuli as heat and drought, or other departures from the optimum, have been suggested as the agencies which induce it. They may indeed play a part in determining its onset, but the phenomenon must be genetic as well as environmental, for some species are notorious migrants while others are not, depending to some extent no doubt on whether they are euryplastic or stenoplastic forms. The latter, adjusting themselves accurately to local conditions, will not benefit from migration.

H. B. D. Kettlewell (1952) has suggested a genetic model which shows how the tendency to migrate could be controlled. Though over-simplified, as such speculation is bound to be, it may rather closely represent the type of mechanism involved.

Migration usually takes place in the spring or early summer from the south northwards bringing, for example, Mediterranean species to our shores. In some instances, however, Scandinavian insects may migrate south at this time. Kettlewell suggests that a gene *M*, perhaps increasing metabolic rate, produces excess activity and gives rise to migration. The homozygotes *MM* would be essential migrators and would constantly tend to leave their place of origin. It is assumed that the *mm* type are physiologically incapable of migration, or approach that condition, because of a low metabolic rate and perhaps also owing to a reduction in the size or efficiency of the fat-body. The heterozygotes, *Mm*, would be at a greater advantage than either homozygote in being able to migrate or not according to the environmental conditions.

So far the theory is untenable, since it would lead to a constant drain of the *M* allelomorphs from the population. However, as Kettlewell points out, this difficulty has been removed by the steadily accumulating observations which demonstrate the occurrence of a return migration of these species in the autumn. This being generally more widespread and scattered, though canalised in certain places, as over the Pyrenees, had long escaped observation; but it now appears that it may be as considerable in effect as the migrant streams of the spring.

It is to be noticed that the superiority of the heterozygotes over either homozygous class, producing a polymorphism, is an essential of this theory, which fits the known facts quite well. Thus, (1) some species, those which have evolved the necessary polymorphism, are subject to migration while others are not. (2) This takes place on a large scale in certain years only, when the heterozygotes, *Mm*, are stimulated to migrate. (3) Even in other years, some individuals of such species migrate, and these would be the homozygotes *MM*. (4) Yet even in those seasons in which the migratory impulse is strongest, some of the insects remain behind in their place of origin, and it is assumed that these are the *mm* homozygotes. On the whole, there seems good reason to think that some mechanism of this type is involved in the control of migration in the Lepidoptera, while a corresponding situation seems to exist in birds (Lack, 1943).

The Dispersal of Genes

It has already been pointed out that the dispersal of individuals depends principally upon larval movement in those species in which the females are wingless, and that this seems to have been remarkably effective. Here the flight of the males, as in other moths, has two functions, that of bringing the sexes together and of dispersing genes. The wide scattering of the genetic material, within and even between populations, is ensured by the fact that on the average the males emerge in advance of their mates and actively search for them. Moreover, a number of males in addition to the ones which are successful may be attracted to a single female, sometimes from great distances (Chapter 1), for though her scent ceases to be elaborated after mating, the odour usually clings to her during that process. In general, the male can pair a number of times but the female only once, save on rare occasions when her stock of introduced sperm has been exhausted towards the end of her life.

It appears that males on the average fly higher than females, a circumstance which would tend to scatter them. Unfortunately there is very little evidence bearing on this subject. However, I have always obtained a greater proportion of males when using a light-trap at upper windows than on the ground floor, and Bretherton (1950) confirms this observation.

There is, I think, no harm in speculation provided that it is clearly understood to be such. The ‘ attraction ’ of many species of moths to artificial light, and the physiology of this occurrence, have been discussed in Chapter 1: but it may not unreasonably be asked why, in common with some other night-flying insects, they visit lights at all; for these have been available for them only in recent years. Such behaviour may be a purely accidental outcome of their vision and of their nervous responses, or it may to some degree have been moulded by selection. Robinson and Robinson (1950) state that the range of their powerful mercury-vapour traps is only about a hundred yards: by this they must mean that a clearcut response is discernible only for that distance. No observations at present exist capable of deciding whether or not there is a slightly greater tendency for moths to orientate themselves towards an illumination equal to that of bright moonlight than to fly indiscriminately with respect to it. Such a reaction, if it exists, should have the effect of causing them to fly high on moonlit nights. That, if so, they do not continue to rise indefinitely need cause no surprise, since the reversal of a taxis with changing environments is a well-known occurrence. Thus the rapid reduction in pressure, which the ear-drums of moths appear well adapted to detect, might provide the control required to check their ascent. If such a response were principally to involve the males, as well it might since that sex seems the more inclined to fly high, its effect would be to disperse the genes of the species without scattering the individuals too widely beyond their habitat.

The attraction of moths to artificial lights, and the different habits of flight in the two sexes, had long inclined me to speculate along these lines. I was therefore very ready to consider such an hypothesis when Professor A. C. Hardy proposed it to me in a much more developed form than any I had myself envisaged. With the helpful co-operation of the Royal Air Force, for which we were most grateful, he and I made several balloon ascents on dark and on moonlit nights. We attempted to attract moths to a light at different altitudes, using motor-car headlights on the ground as a control. The results have so far been inconclusive, partly owing to the difficulty of ensuring that the rather complicated arrangements which have to be made should coincide with suitable collecting nights. They were not, however, wholly negative (we saw three moths flying at a thousand feet on a moonlit night) and we hope to continue them in more favourable conditions. Should they give positive results, which is conceivable but by no means certain, the rather mysterious attraction of moths to a light would be invested with a new meaning.

CHAPTER 7

PROTECTIVE DEVICES

Cryptic Colour-patterns

The sting of a bee or a wasp is an effective weapon; so too are the biting jaws of certain ants, some species of which will attack a human intruder ferociously and can readily draw blood, as I myself have found in the arid interior of Australia. Moths are not provided with the means of such active defence. Their safety lies principally in concealment, but sometimes in the possession of a disagreeable taste or smell or of irritating hairs avoided by an enemy once their unpleasant qualities have been learned.

Birds are the chief predators against which such measures are effective, but bats and spiders are also destructive to the Lepidoptera, while mice certainly kill great numbers of the pupae of some species, especially those which lie among tangled herbage, as for instance the Scarlet Tiger, *Panaxia dominula* L., Hypsidae. There are a few species of dark inconspicuous colour which hide themselves in crevices or among any available litter of leaves and sticks. Thus the rare and much overlooked Waved Black, *Parascotia fuliginaria* L., Plusiidae (Plate 4), scuttles away to such places immediately the wings have dried after emergence from the pupa. Indeed, owing to this habit, it is quite difficult to obtain a specimen in good condition even when bred in captivity, for the scales are rather loosely attached, so that the moth is often damaged in attempting to secrete itself. However, the imagines of most moths, like their larvae, rest upon trees or herbage, or they may expose themselves freely upon bark, wood, or stones, trusting to their colour-pattern for concealment. The manner in which this is achieved in such circumstances merits a brief examination.

A green insect when sitting on leaves or among grass is generally quite well hidden. Rather curiously, though many larvae adopt this apparently simple device, but few Lepidoptera do so in the imago state; in Britain these principally belong to the Cymbidae (Plate 16), and the Emeralds among the Geometridae (Plate 1). The green colouring, though pigmentary in both, is chemically different in these two groups. In one other genus of green moths, *Procris*, Zygaenidae, the Green Foresters (Plate 26), it is, however, produced by structural means like the colours on a soap-bubbles (pages 4-5).

Many green larvae give rise to brown-winged adults which derive protection by resemblance to dead leaves or by other means. A good instance is provided by the Festoon, *Cochlidion avellana* L., Heterogeneidae (Plates 2 and 16). The reverse situation also occurs, for the larva of the brilliantly green Blotched Emerald, *Comibaena pustulata* Hufn., is brown. This circumstance draws attention to the fact that the caterpillar and imago, even of the same species, lead such entirely different lives and bear such dissimilar relationships to the general environment, that the methods by which they escape their predators are usually quite distinct, just as it has already been pointed out that their variation is independently controlled in these two phases of their lives.

The young larva of the Blotched Emerald, and of several related species, escapes detection by disguising itself with the scales of oak-buds. It attaches these by spinning silk on one side of them. This is then entangled by numerous hooked bristles scattered over its body, and these hold the scales in place.

A resemblance to brown withered leaves is of course an appropriate means of concealment at all times of year, whether the wings are carried flat or, as in some Hydriomenidae and Selidosemidae, erect over the back like a butterfly (Plate VII). This type of protection is developed to an extreme degree in the Lappet, *Gastropacha quercifolia* L. (Lasiocampidae), in which when at rest the fore-wings are carried at the angle of a sloping roof while the hind pair are held flat. Their colour is purplish brown and the effect produced is remarkably like a bunch of withered leaves, an illusion heightened by the long palpi which give the impression of a short stalk. It is noteworthy that many of the moths which emerge in the autumn have the light brown or golden hue of autumnal foliage (Plate 25): a predominant shade in the 'Sallow Moths' which appear at that season.

Some imagines resemble a piece of stick with extraordinary accuracy, and occasionally the markings also represent its broken ends (Plate 20). Others are adapted by habit and colouring to wrap their wings around a narrow twig or to sit on small stems, like the Yellow Horned, *Achlya*

Plate 11. GENETICS: SELECTION EXPERIMENTS

1
COTHILL
BERKSHIRE

2
COTHILL
BERKSHIRE

3
COTHILL
BERKSHIRE

4
COTHILL
BERKSHIRE

5
COTHILL
BERKSHIRE

6
CUMBERLAND

7
CUMBERLAND

8
CUMBERLAND

9
CUMBERLAND

10
CUMBERLAND

1-5. Scarlet Tiger, *Panaxia dominula:* 1 typical, marked with cellulose paint, 2 *bimacula,* 3-5 *medionigra;* 6-10. Currant Moth, *Abraxas grossulariata:* 6 typical, 7-8 *semi-lutea,* 9-10 *lutea*

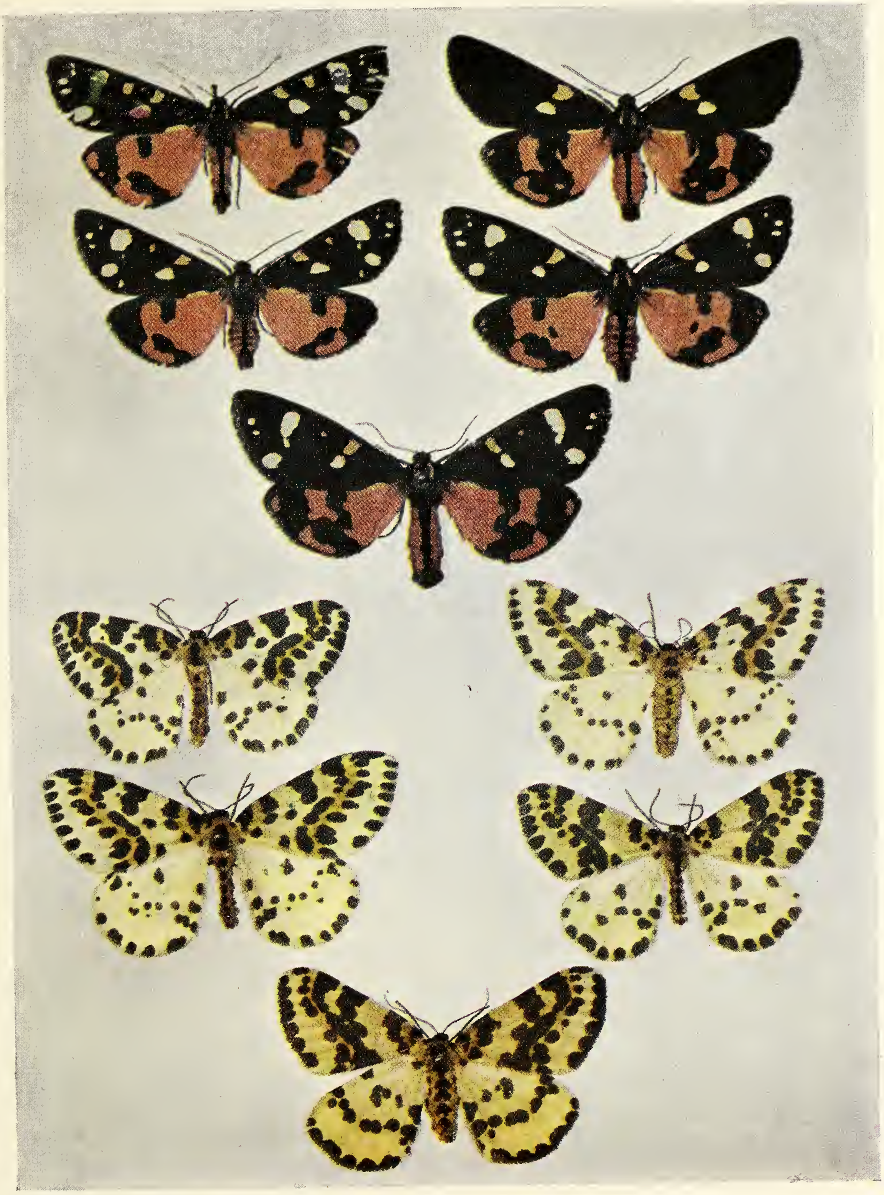


Plate 11

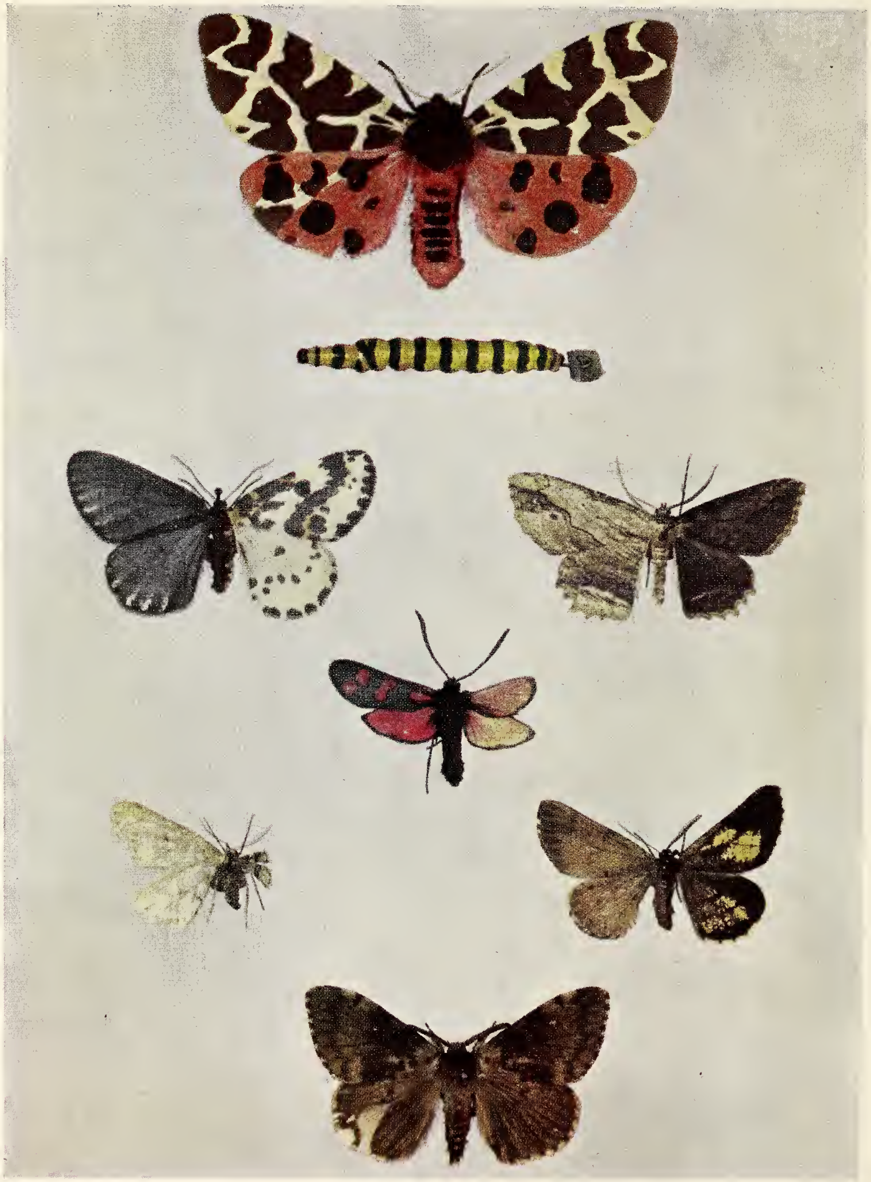


Plate 12

Plate 12. SOMATIC VARIATION AND SEX-INTERGRADES

1
SUSSEX

2
MIDDLESEX

3
HUDDERSFIELD
YORKSHIRE

4
HOLLOWAY
MIDDLESEX

5
SUSSEX

6
OXFORD

7
OXSHOTT

8
ENGLAND

1. Garden Tiger, *Arctia caja,* showing homeosis; 2. Cinnabar, *Hypocrita jacobaeae,* larva with spiral segmentation; 3. Currant Moth, *Abraxas grossulariata,* somatic mosaic; 4. Waved Umber, *Hemerophila abruptaria,* gynandromorph and mosaic; 5. Six-spot Burnet, *Zygaena filipendulae,* showing homeosis; 6. Winter Moth, *Operophtera brumata,* gynandromorph; 7. Bordered White, *Bupalus piniarius,* gynandromorph; 8. Gipsy Moth, *Lymantria dispar,* intersex

flavicornis L., Polyplocidae (Plate 25), an inhabitant of birch thickets, which emerges before the leaves in early spring. Here also must be mentioned those moths which match fragments of wood. It will be realised that such adaptations bring about *convergence*: a superficial similarity between species which are not closely related and whose fundamental structure may consequently be very different. Thus the Waved Umber *Hemerophilia abruptaria* Thn., Selidosemidae, and the Small Waved Umber *Horisme vitalbata* Schiff., Hydriomenidae, chosen to illustrate this type of concealment (Plate 20), belong to different families, though they are often mistaken for one another. A striking instance of convergence is provided by those marsh moths whose colour-pattern fits them to rest upon reeds: one of them is shown in its natural environment in Plate 25, while a group of these insects is assembled on Plate 17 (figures 1-5, 7-10). They belong to two subfamilies of the Caradrinidae and to seven different genera, which are separated by others having an entirely different appearance. Furthermore, the larva of one of these reed-like moths, the Powdered Wainscot, *Simyra albovenosa* Goeze (figures 10 and 12), is dark and hairy and feeds externally. It is extremely distinct from the remainder, for example the Southern Wainscot, *Leucania straminea* Treits (figures 9 and 11), which is smooth, pale and feeds internally in reed-stems, in spite of the similarity of the imagines. Indeed the Powdered Wainscot is more closely related to the Grey and Dark Daggers, *Apatele psi* L. and *A. tridens* Schiff., shown at the foot of the same Plate, as the appearance of the larvae (figures 12, 15 and 16) suggests.

Several moths are beautifully adapted to sitting on the trunks of pine-trees, like the Pine Hawk, *Hyloicus pinastri* L., Sphingidae (Plate 15), and the Pine Beauty, *Panolis griseo-variegata* Goeze, Caradrinidae, which resemble respectively the dark bark and the reddish marks upon the trunk. The Pine Hawk larva, on the other hand, has to conceal itself among the pine-needles on which it feeds. Up to and including the penultimate stage, it has a green ground-colour subdivided by long light lines of about the correct thickness to give a needle-like appearance. The fully-grown larva is, however, too large for such a technique to be effective; consequently its pattern is so altered as to break up its shape by a confusing design of green, brown and white (Plate xv).

The resemblance to needle-like foliage has been achieved by several other species of larvae and by some imagines, of which the nearly extinct Frosted Yellow, *Isturgia limbaria* F., Selidosemidae, provides a good example. This is, or was, found among broom bushes, and when at rest with the wings held above the back only the underside of the posterior pair is to be seen. On examining the specimens illustrated on Plate 29 it will be appreciated how well protected the insect would then be.

There are many instances in addition to the Pine Hawk in which the appearance of a larva changes during growth, to accord either with the passage of the seasons or with the conditions imposed upon it by its altered size and habits. Thus the Large Emerald, *Geometra papilionaria* L., Geometridae, hatches from the egg in the late summer and feeds, chiefly on birch, until autumn when it hibernates on the twigs. At this period of its life it is reddish brown with some green markings, a colour-pattern which harmonises well with its surroundings. In spring, when it awakens, the amount of green on the body increases until it almost replaces the brown, so that the creature is still concealed as it sits upon the young leaves. Also the larvae of the Emperor, *Saturnia pavonia* L. (Plate 18), are at first blackish, while still small enough to rest upon the stems of heather and other food-plants, but they become bright green, with a cryptic pattern of light dots, when grown so large that they would no longer be hidden as dark objects upon a branch (Plates 7 and 19). So perfectly does their colour then conceal them that when they are two inches or more in length anyone but an experienced naturalist must make quite a careful search to find these larvae as they sit fully exposed upon the heather. It is a curious fact that though men who suffer from red-green colour blindness* fail to distinguish sharply between red and green they can, on the other hand, discriminate shades which appear alike to those with normal sight: a reaction used in the Ishihara tests for colour-blindness. To such people the Emperor larva loses its cryptic colouring and stands out clearly from its background as a yellowish instead of a green object. Indeed, I have visited moors where this moth is common, in company with such men, and found that they could point out these larvae when 20 or 30 yards distant. In ourselves, at any rate, red-green colour blindness is inherited on a unifactorial basis, and therefore susceptible to direct selection. Though normally a handicap, were it to arise in an appropriate predator it could confer an immediate advantage to its possessor and, provided the gene concerned did not have other disadvantageous effects sufficient to counterbalance this, it would spread through the population, undermining at a single stroke the usefulness of a protective colour-pattern which had been evolved in its prey. Certainly no such occurrence has been detected, but the possibility of it should be kept in mind in considering the evolution of protective coloration.

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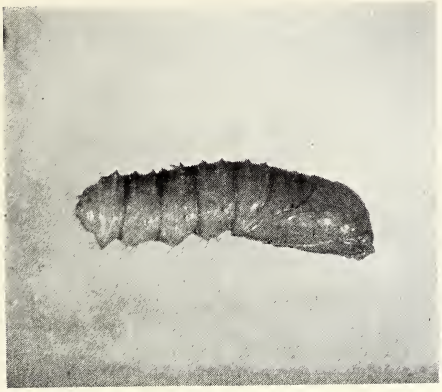
*The condition, being recessive and totally sex-linked to the X-chromosome, is rare in women even though occasionally expressed when heterozygous.

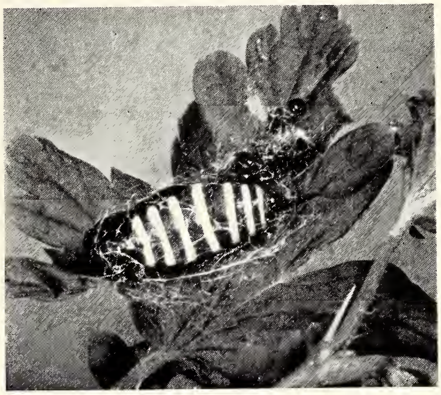
Many small larvae immediately drop from their food-plant when disturbed, retaining connection with it by a thread of silk, which they spin with great rapidity (Plate XVI), and they must be nearly safe from capture by birds when thus swinging in the air. Later they can clamber back along their life-line and so regain their food. Though some quite large larvae can perform this feat, it becomes more difficult with increasing size. Consequently in their later stages they often cling firmly when a bough is lightly shaken and trust to their cryptic colouring for protection. The ' looper caterpillars ' of the Selidosemidae and other groups often have the habit of grasping a twig or leaf-stalk with the two pairs of claspers remaining at the posterior end of the body and holding themselves out rigidly at an angle so as to resemble a green or brown stick (Plate 19). This is the habit of the Waved Umber in its later stages (on Plate XVI it is shown looping).

A great assortment of natural objects has been copied by moths in order to conceal themselves in their larval and imaginal stages. Among these, lichen may especially be mentioned; the perfection sometimes attained in representing it is illustrated by the normal specimen of the Peppered Moth, *Biston betularia* L., Selidosemidae, sitting on light-coloured bark shown on Plate XXIII. The lichen-like pattern may be recognised in a number of the species illustrated in this book: for instance Plate 32, figure 5, and several of the specimens in their normal forms on Plate XXIV. They all sit fully exposed with outspread wings.

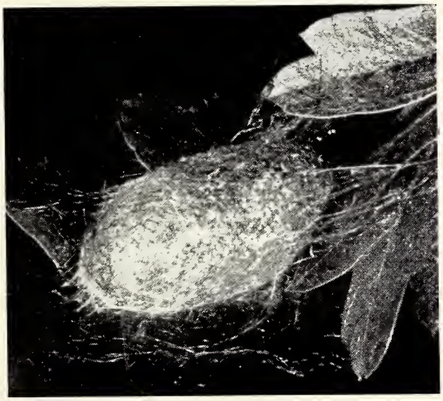
Trees, leaves, and plants in general, do not markedly change their appearance from one part of the country to another, so that to resemble them poses few problems of geographical variation. The extraordinary situation which has resulted from the blackening of vegetation due to industrial pollution raises new issues which will be separately considered in Chapter 13. When, however, moths are adapted to sit upon rocks, it is necessary they should adjust themselves to local conditions. How well they succeed is shown by the examples of the Annulet, *Gnophos*



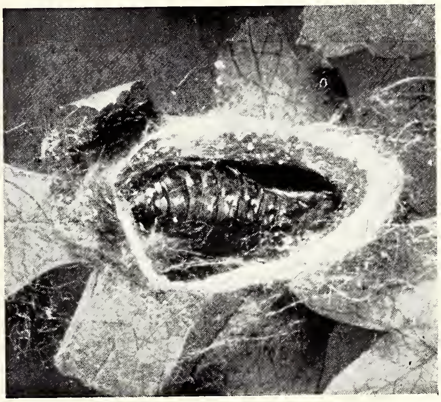
1. Common Swift, *Hepialus lupulinus*, pupa (X 2)



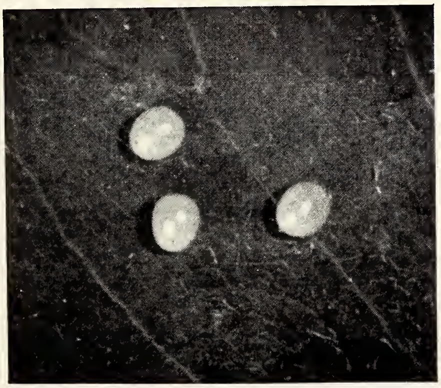
2. Currant Moth, *Abraxas grossulariata*, pupa (X 2)



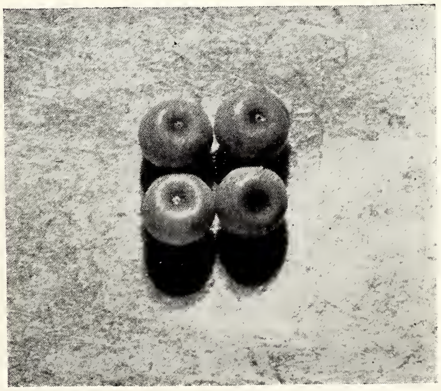
3. Gold-tail, *Euproctis chrysorrhoea*, cocoon (X 2)



4. Gold-Tail, *Euproctis chrysorrhoea*, cocoon opened (X 2)

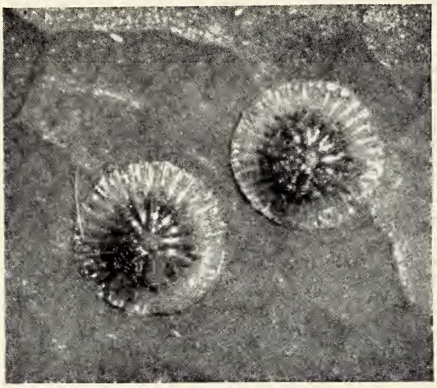


5. Poplar Hawk, *Laothoe populi*, eggs (X 5)

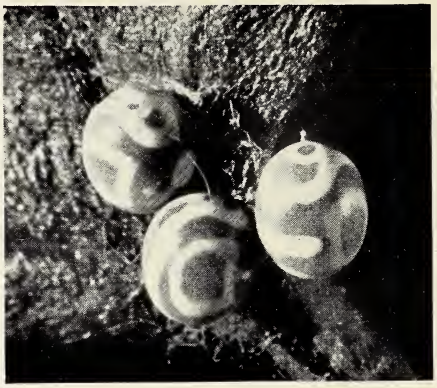


6. Pale Tussock, *Dasychira pudibunda*, eggs (X 10)

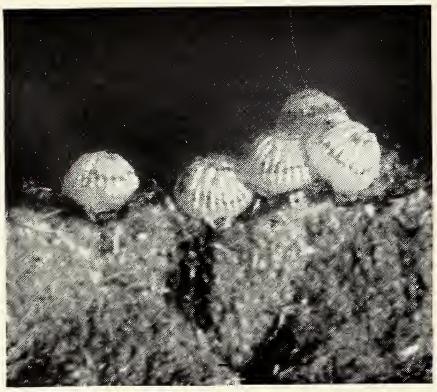
Plate IX. EGGS AND PUPAE



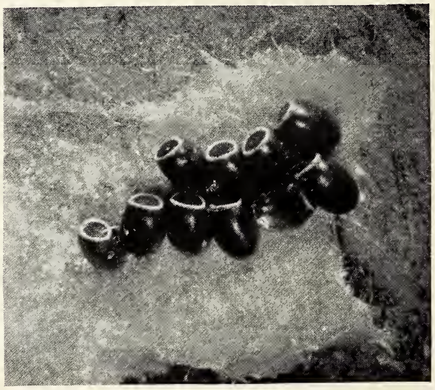
1. Green Silver-Lines, *Bena prasinana* (X 15)



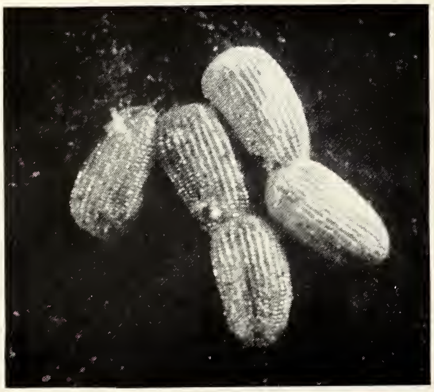
2. Lappet, *Gastropacha quercifolia* (X 10)



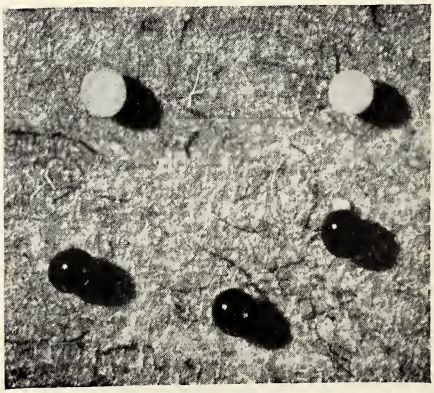
3. Angle-shades, *Phlogophora meticulosa* (X 15)



4. Large Thorn, *Ennomos autumnaria* (X 18)



5. Dotted Border, *Erannis progemmaria* (X 25)



6. Common Swift, *Hepialus lupulinus* (X 12)

Plate X. Eggs

obscurata Schiff., Selidosemidae, and of the Tawny Shears, *Hadena lepida* Esp., Caradrinidae, illustrated on Plate 30. In particular, the Annulet, whitish from the chalk, red-brown from the sandstone of South Devon and blackish from dark soil in Surrey, represents one of the most remarkable instances of adjustment to background ever illustrated. The Tawny Shears, from the chalk, from brownish rocks in Cornwall, and from the dark ones of the Isle of Man, is only slightly less striking.

A number of moths adopt the effective device of combining cryptic and 'flash' coloration. This can be illustrated by two examples shown on Plate 5. Both of them have dull-coloured fore-wings. The Red Underwing, *Catocala nupta* L., Plusiidae, is remarkably well hidden when sitting on tree-trunks, walls, or rocks, while the Large Yellow Underwing, *Triphaena pronuba* L., Caradrinidae, is also inconspicuous when at rest among tangled grass or low herbage. If disturbed, however, they take to the wing readily, when the scarlet or yellow of the hind-wings, previously out of sight beneath the front pair, produces a sudden flash of colour which, combined with their irregular flight, makes them difficult to follow; while the sudden disappearance of the colour on settling is also confusing. These species belong to large genera all the members of which adopt this type of protection.

An effective method of concealment is also obtained not by matching the background but by a confusing arrangement of the pattern or by the presence of contrasting oblique stripes which mislead the eye and disguise the outline of the insect. One example of this has already been provided by the last instar of the Pine Hawk larva, and the illustrations in this volume will be found to supply others: among them, attention may be drawn to the Green Silver-lines, *Bena prasinana*, Cymbidae (Plate 16), and the male Common Swift (Plate VII), as imagines, or to the Privet Hawk, *Sphinx ligustri* L., as a larva (Plate 21). Moreover, a single bold line can sometimes be made to cut an insect in halves as it were, by which its apparent shape may be so altered as to produce an object which does not resemble a moth; see the Blood-vein, *Calothysanis amata* L., Sterrhidae, illustrated on Plate 16. A longitudinal lateral line often achieves this result in larvae (*e.g.* The Bordered White, *Bupalus piniarus* L. Selidosemidae (Plate 7). It is usual for cryptically coloured animals to be paler below than above, an arrangement which tends to obliterate their shadow and so make them inconspicuous. In a few larvae, for example that of the Eyed

Hawk, *Smerinthus ocellatus* L., Sphingidae, this design is reversed because they rest with the dorsal side downwards.

A judicious arrangement of the pattern may also serve to draw attention away from the vital parts of the body. The eye of an insect is not only itself vulnerable but, being situated on the head, indicates a vulnerable point for attack. Great numbers of Lepidoptera have therefore developed eye-like marks near the edge of the wings, where they can be damaged without serious effects, as in the male Vapourer, *Orgyia antiqua* L., Lymantriidae, illustrated on Plate 1. I have myself seen a lizard pick out the ‘ eye-spot ’ from the wing of a Small Heath butterfly, and I do not doubt that similar devices in moths also serve on occasion to misdirect the enemy. I suspect, however, that the great ‘ eyes ’ in the centre of the wings of an Emperor moth (Plate 18) perform a somewhat different function. The most dangerous period for any butterfly or moth must be that during which the wings are expanding and drying after emergence from the pupa. The insect is then not only helpless, being incapable of flight, but its protective colour-pattern is not yet unfolded. During the early stages of this process these ‘ eye-spots ’ are accentuated by the puckering of the wings, which gives the Emperor moth an appearance that may well terrify potential predators. It is likely that some of the wing-markings of other species may also be of special assistance to them at this the most vulnerable time of their lives. The ‘ eye-spots ’ on the larva of the Elephant Hawk, *Deilephila elpenor* L., Sphingidae (Plate 21), enhance the alarming result produced when the creature swells out its anterior segments, with a decidedly snake-like effect, as it does when danger threatens.

In contrast with the device already mentioned, in which a special arrangement of the pattern gives the impression of an irregular outline, the shape of some species is in fact unusual and this serves to accentuate their resemblance to natural objects. For instance some larvae are curiously humped and angled, as is the Pebble Prominent, *Notodonta ziczac* L. (Plate 19), while in the Hook-tips, Drepanidae (Plates 2 and 26), the apex of the fore-wings is generally elongated and curved. The shape produced is an unusual one in moths and adds greatly to their resemblance to dead leaves. However, one member of the Drepanidae, the Chinese Character, *Cilix glaucata* Scopoli, escapes its enemies in an entirely different way: by making itself conspicuous and copying a bird dropping (Plate 2), an object likely to be avoided by any predator.

Consequently the usual concealing shape of this group, with the hooked fore-wings, has been lost in this species, which superficially bears no resemblance to the rest of this family; yet the singular structure of its larva, in which the anal claspers are absent, clearly indicates its affinity (Plate 2).

Many larvae which feed at night and remain hidden by day are not protectively coloured. Indeed, these are often dark or blackish and certainly do not match the plants which they eat. Their colouring may be interpreted in either of two ways. It may be a ‘ subsidiary ’ effect of certain genes which, not being exposed to the visual choice of predators, is unaffected by selection. For of course the deposition of pigment may take place in circumstances in which the actual colour produced can have no survival value, as in the pigments of the internal organs: for instance, the black lining of the body-cavity (coelom) of many Vertebrates. Alternatively it may be that these larvae do, in fact, derive some benefit from being dark, as they will be much less conspicuous in twilight than if unpigmented and whitish; for when the luminosity is reduced, tone remains for a time important when colour is no longer perceptible. I am inclined to favour this latter hypothesis, for many larvae never expose themselves, feeding, and eventually pupating, internally in wood or stems or below ground, and these are white far more often than can be ascribed to chance. The larva of the Goat Moth, *Cossus cossus* L. (Plate 6), though living in burrows in solid wood, is mahogany-coloured on the back, but it leaves the tree in which it has fed and wanders a considerable distance in search of a place to pupate : unlike the Clearwings, which remain in their burrows up to the imaginal stage, and have whitish larvae (Plate XVI).

It should be mentioned that green or otherwise cryptically coloured larvae which pupate in the ground lose their resemblance to their food-plant and become dark or blackish at the time that they descend to search for a place where they can bury themselves. On the other hand, some larvae which feed and pupate out of sight, as the Wainscots, which do so in reed-stems (Plate XVII), are dull-coloured; this presumably is a ‘ secondary ’ effect of the genetic and physiological processes of the body unchecked by selection for coloration.

An unusual method of concealment is adopted by the larva of the Portland Moth,* *Actebia praecox* L., Caradrinidae (Plate 1), and some other coastal species. This lives in a vertical tunnel in the sand. The mouth of the tube collapses after the larva has entered (probably its movements ensure this) and its retreat is then invisible. Towards evening it crawls out to feed upon dwarf sallow, wormwood and some other seaside plants, and its colour blends with that of the sand over which it passes. It is shown beside the entrance to its burrow in Mr. Beaufoy's beautiful photograph on Plate 6.

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*The name commemorates a former Duchess of Portland, not a locality for the species.

Thick chitin normally ranges in colour from brown to blackish. Consequently most pupae are of these shades, whether concealed from view below the soil, among dead or living leaves, or in an opaque silken cocoon. Those of the Bordered White, which lie under moss in pine woods (Plate VIII) are an exception, having bright green wing-cases. Dark chitin is less pervious to water-vapour than is light, so tending to prevent desiccation. Consequently pupae living in very dry situations, for instance when buried in sand, are particularly dark.

Most pupae protect themselves in one way or another, yet curiously enough some do not appear to do so at all. Reference has already been made to those of the Scarlet Tiger which lie among litter on the ground with only a few threads of silk about them. There is considerable evidence that this species suffers a relatively small amount of elimination up to the end of larval life, and that the high proportion of larvae to imagines is adjusted to counterbalance the loss experienced in the pupal and imaginal stages.

Most, perhaps all, subterranean pupae are enclosed in a cocoon, sometimes tough but sometimes exceedingly frail. This is lined with silk and forms a chamber in the soil (Plate VIII), but is often so easily damaged that it may collapse and escape attention when found. Such weak cocoons are probably of use only in protecting the pupae from mould and bacteria.

However, some cocoons are strongly constructed, the silk being hardened with calcium oxalate or by other means, and they are then an effective deterrent to most predators, including small birds, particularly if attached to leaves or thin stems which do not provide a firm background against which the structure can be broken open or upon which the enemy can perch. Indeed, G. D. H. Carpenter found a colony of the Burnet Moth, *Zygaena filipendulae* L., in which some of the cocoons had been attached to a wire fence and others to tall grasses. All those on the fence had been pecked open by birds, which were seen to cling to it and successfully attack them, while those on the grass-stems, on which birds could obtain no foothold, escaped. Possibly the cocoon of the rare Waved Black (Plate XI), which is extremely difficult to see, gains advantage also from its mobility, for it hangs like a hammock attached at the two ends by silken threads.

Some cocoons are much too resistant for the moth to force its way out on emergence except by special means. The curious devices then employed have been studied in some detail in a few instances. For example the Puss Moth, *Cerura vinula* L., Notodontidae, constructs a hard cocoon of silk, with which fragments of wood and sawdust are so interwoven that it is almost invisible when placed, as it normally is, in a crevice of bark. On emergence, the imago softens the wall of the cocoon with strong caustic potash and then uses the anterior end of the pupa-case for cutting its way out. This is appropriately shaped for the purpose and provided with hooks by which it is held on to the head of the moth: subsequently it is pushed off by the legs.

One of these hard cocoons, that of the Waved Umber, is shown on Plate XVII. It is so plastered on to the surface of the branch to which it is attached that it is extremely difficult to see.

Some cocoons have quite complicated structures. That of the best-known species of Silk Moth, *Bombyx mori* L., consists of three silken shells, the outer loose and fluffy, the middle strong and tough, and the innermost thin and papery. It is from the intermediate layer only that commercial silk is obtained. This can be wound off as a single unbroken thread about 1,500 feet in length. The moth seems to have become extinct in the wild state but is of course maintained in domestication in many countries and, before the invention of artificial silk, was the basis of an immense industry. Several other species still existing in nature are also used in the production of commercial silk, but to a lesser degree.

An even more elaborate type of defensive cocoon is constructed by our own Emperor Moth. It is pear-shaped with an exit for the imago at the narrow end. This takes the form of a short tube, near the bottom of which is a ring of stout spines converging to a point. Since these are directed outwards they can easily be pushed aside by the moth within, but they form an effective barrier to any intruder. The arrangement is well shown in a photograph by Mr. Beaufoy on Plate XI, in which one of these cocoons has been bisected.

Warning Coloration and Mimicry

The protective devices so far described are all of the concealing or 'cryptic' type, except for such pupae as are housed in cocoons strong enough to withstand the onslaught of most predators: and indeed the majority of these are also carefully hidden. Quite a different situation is encountered in those species which are inedible or unattractive to predators by reason of an unpleasant taste or smell or the possession of irritating hairs. Such insects advertise their distastefulness by means of 'warning coloration.' This generally takes the form of some simple conspicuous pattern by which they may be recognised, and consequently avoided by potential enemies, once their unpleasant qualities have been experienced. They are often tough and leathery, so that they may actually be pecked at by a bird, or seized by some predaceous insect, such as a wasp or dragonfly, without serious damage before being rejected. Since many of them readily exude repellent juices when handled, these at any rate, are quickly cast aside often almost unharmed.

A characteristic example of warning coloration is provided by the brilliant Cinnabar Moth, *Hypocrita jacobaeae* L., Arctiidae, which is a familiar object in the southern counties of England, and some of the northern ones, in May and early June. The scarlet hind-wings and blackish-green fore-wings, also marked with scarlet, make this insect conspicuous, for its flight is slow and it does not attempt to conceal itself. The larvae (Plate 23) are banded with black and yellow and feed upon ragwort, often in hordes which denude it over large areas. They are easily seen, especially when they have partly stripped the plants of their leaves. Such 'protected' larvae as these are indeed frequently gregarious: a habit from which they derive considerable advantages. For a predator which receives a single lesson of inedibility by molesting one specimen is particularly liable to apply it to the whole group; moreover, if the protective device involves the production of an unpleasant odour, this will be accentuated if the larvae live together in close company.

We cannot safely rely on our own senses in assessing the amount of protection afforded by taste or smell, as the perceptions of an insect's enemies may be much keener than ours and different in quality. It has already been remarked that the extraordinarily powerful attractive odours emitted by moths are undetectable by us, and though the reactions to stimuli of a bird may well be much more like our own than those of an insect, the fact serves to remind us that the human sense of smell, and therefore what we generally call ‘ taste,’ is greatly atrophied. It is not surprising therefore that some moths which appear odourless and almost tasteless to us are violently rejected by birds and by other mammals when fed to them. However, if the flavour of an insect is disagreeable to us, and especially if it be caustic, as that of the Aristolochia Swallowtail Butterflies of the genus *Polydorus*, it is very likely to be unpalatable also to potential predators. Therefore I personally have made a habit, which I recommend to other naturalists, of eating specimens of every species which I study.

For example, the Currant Moth, *Abraxas grossulariata* L., Selidosemidae, has to me an unpleasant, bitter flavour in all its stages and it is known to be distasteful to insect-eating birds. The semi-gregarious larva (Plate VI), white with black dots and reddish marks, is quite conspicuous; while the pupa is a striking object, being black with bright yellow transverse bands. It is attached to the underside of leaves by a cocoon, but this has the unusual quality of being thin and transparent so as clearly to reveal the pupa within (Plate IX). The moths, too, immediately catch the eye whether at rest or flying slowly, as is their habit; for they are white, marked with black spots and a yellow band (Plate II, figure 6). In the country they feed upon a variety of plants, including blackthorn (*Prunus spinosa*) and ling (*Calluna*), but in gardens they have become a serious pest of gooseberries and currants.

It is probable that many moths with warning coloration are protected by an unpleasant smell, which our own feeble perception of scent cannot detect. Indeed, the behaviour of bats and insectivorous birds in captivity when given such species strongly suggests that they avoid them on this account. However, the odour of the Goat Moth larva is so pungent that it is retained for years by a piece of wood into which one of them has bored. Moreover, the gregarious larva of the Buff-tip, *Phalera bucephala* L., Notodontidae, apparently produces a rank, disagreeable smell detectable to some people, though not to myself.

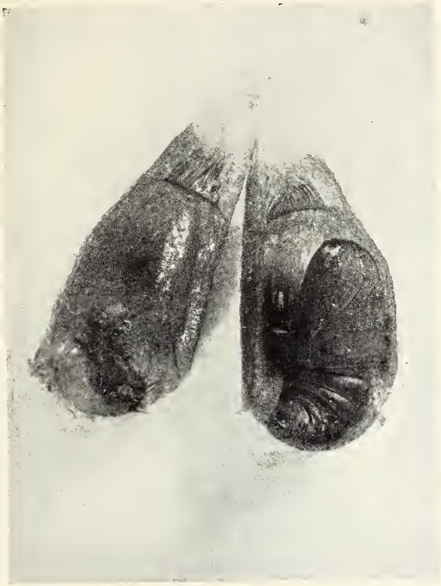
The possession of thick hair is a frequent means of defence in the larval stage. Hairy caterpillars are sometimes gregarious (Plate 23), and are often very conspicuous (Plate 22). In some species the hairs are barbed and may cause considerable irritation, especially if transferred to the face and eyes. In general, hairy larvae should be handled with caution and few birds attempt to eat them.

Some moths have developed this form of protection to a high degree, and on certain regions of the body their larvae grow hairs especially modified for defence. A good example of the kind is provided by the Yellow-tail, *Euproctis chrysorrhoea* L.=*similis* Fuessly, Lymantriidae, illustrated in Plate 24. The larva of this moth is a striking object and it feeds in full view upon hawthorn and other plants. On examining a specimen it will be found that the hairs growing from certain dark patches on the back take the form of barbed spicules; these are shown magnified in Plate XVI. They are attached point downwards and consequently break off extremely easily. Those who incautiously handle them may develop a severe attack of nettle-rash.

These spicules are produced by the larva but, by an extraordinary series of adaptations, they are made to serve as a protection throughout the life of the moth. The pupa is enclosed in a silken case attached to the food-plant. It is avoided by most insect-eating birds since some of the irritating spicules are spun up among the silk. However, the old larval skin lying inside the cocoon at the tail-end of the pupa is the chief repository of them. The imago is a white insect with a tuft of yellow hair at the end of the abdomen. When a female moth emerges, she especially collects the larval spicules by means of this tuft, which she repeatedly opens and closes fanwise while sweeping it over the shrivelled larval cuticle. The tuft thus becomes charged with the barbed shafts and they are retained by the structure of the yellow hairs of which it is composed, for these are branched and spined in such a way as to entangle them.

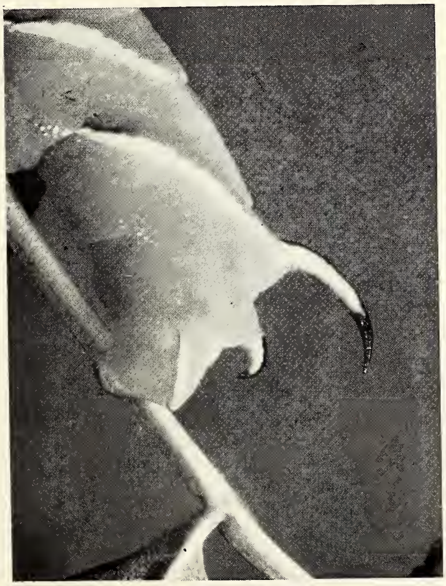
For this reason the yellow tail of this moth is, in the female sex, as irritating and as much to be avoided as the larva, and she puts it to good use in protecting her eggs. These are laid in small heaps and are at first sticky. After depositing each pile she presses down her golden tail upon it, when some of the tuft adheres to the mass. Consequently the eggs are hidden by yellow down (Plate 24) containing barbed spicules transmitted from the larval stage.

These adaptations directed to the preservation of the eggs are restricted to the female sex. The yellow tuft of the male imago is much smaller than that of the female and, unlike hers, is composed of straight hairs of simple structure unsuited to retain the barbed spicules. Moreover, the male makes no effort to collect these, but on emerging breaks straight out of the cocoon to dry his wings, without pausing to

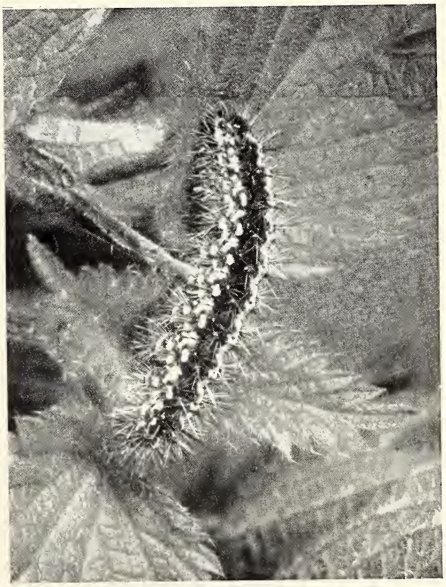


1. Emperor, *Saturnia pavonia*, cocoons (X 1.5)

2. Waved Black, *Parascotia fuliginaria*, cocoon (X 2)



3. Privet Hawk, *Sphinx ligustri*, larva with two horns (X 2)



4. Scarlet Tiger, *Panaxia dominula*, larva (X 1.5)

Plate XI. LARVAE AND PUPAE

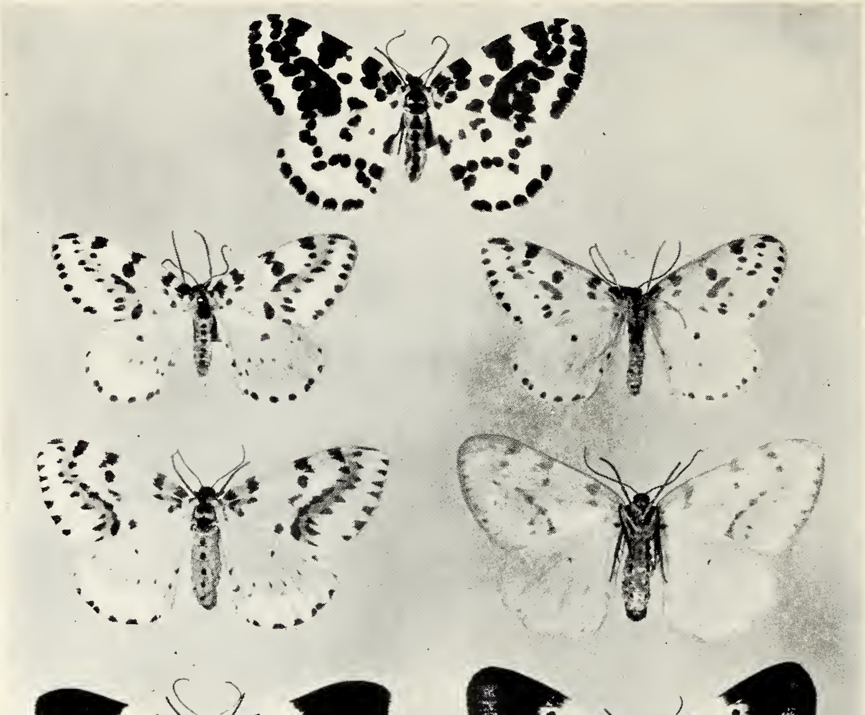


Plate XII

CUMBERLAND

2
CUMBERLAND

3
underside
ROXBURGH

4
LANCASHIRE

5
underside
LANCASHIRE

6
YORKSHIRE

7
YORKSHIRE

8
CUMBERLAND

9
CHESHIRE

10
FERMANAGH

11
BUCKINGHAMSHIRE

1-7. Currant Moth, *Abraxas grossulariata;* 1. typical, 2 and 3, autosomal recessive, 4 and 5, sex-linked recessive, 6. recessive melanic, 7. recessive melanic plus sex-linked recessive; 8 and 9. November Moth, *Oporinia dilutata:* 8. typical, 9. sex-linked recessive; 10 and 11. *Oporinia christyi* sweep the end of his abdomen over the remains of the larval skin. Thus he lacks protection himself and relies for his safety upon using the same colour-pattern as the female, in which it is a warning of real danger. This is an instance of mimicry (page 94); indeed it is carried beyond mere appearance to a similarity of behaviour important when danger threatens. When at rest only the fluffy white wings and thorax are to be seen, but if disturbed both sexes raise the abdomen and expose the yellow tail (Plate 24): a warning movement which potential enemies probably learn to recognise in spite of the fact that it is as often spurious as genuine, for males and females are in approximate equality.

Here we have an unusual situation in which one sex derives protection by mimicking the other. Much more often mimicry involves a resemblance between distinct species, but it is especially a phenomenon of the crowded life of the tropics and sub-tropics and is much rarer among the Lepidoptera of the temperate regions. The most notable instances are provided by those moths which copy bees, wasps, and other stinging or biting forms. On emergence from the pupa their wings are, as usual, opaque owing to the presence of the coloured scales. These, however, are so loosely attached that they are lost the first time that the wings are vibrated, leaving only the clear wing-membrane like that of their ' models.' Mr. Beaufoy has skilfully succeeded in photographing one of these mimetic moths, the Broad-bordered Bee-hawk, *Hemaris fuciformis* L., Sphingidae, both before and after the loss of its scales (see Plate v). This species certainly has a strong resemblance to a bee when at rest, though the flight of the two insects is very different, that of the moth being darting and hovering.

Two groups of British moths extremely remote from one another in relationship have independently acquired this type of mimicry. These are the Bee-hawks to which reference has just been made, and the true Clearwings, the Sesiidae. The convergence (page 94) involved has produced striking results of such similar type that the early entomologists were completely deceived and incorrectly assumed a close affinity between these insects. The Sesiidae are in fact much the more primitive: one of the larger species, the Hornet Clearwing, *Sesia apiformis* Cl., is shown on Plate 25. It evidently bears a fairly convincing resemblance to a hornet and is, at any rate, superficially unlike a moth.

The existence of a mimic is clearly a threat to the safety of its model, whose conspicuous warning colour may too often come to be associated with palatable rather than dangerous or unpleasant qualities. When this occurs, the mimic also tends to defeat its own ends, gradually losing as it becomes common the advantage it possessed when rare. Thus its numbers must be so balanced against those of its model as to secure the maximum possible benefit. In general, this means that a mimic must be much less common than its model; but it can, and generally does, escape from that impasse and increase its total population by evolving polymorphic forms, some or all of which copy different species. Their proportions will then be adjusted until they each possess an equal advantage. Very curiously, however, the Bee-hawks and Clearwings are not polymorphic. The reason for this is obscure, but possibly the extreme transformation of the superficial characters of moths needed to produce a resemblance to bees, wasps and the like, is too great to be determined by one or two major genes which can act as a switch in controlling alternative forms (pages 64-6, 69).

The mimicry so far mentioned is of the Batesian type: that in which palatable species derive an advantage by copying inedible or dangerous ones. Evidently it is also worth while for protected species not only to advertise their qualities by means of an easily recognisable warning colour-pattern but to resemble one another so that a single lesson of inedibility may have as wide an application as possible: this is called Müllerian mimicry and is seen in the striking black and yellow banding of the wasps. How far it is operative in British moths it is difficult to say; but the general correspondence between the Cinnabar and the Burnets (which both have red hind-wings and dark fore-wings with red markings), and between several of the Tiger Moths (having dark fore-wings with white spots and red hind-wings with black spots), may well be of this type. The aim of Müllerian mimicry is to produce uniformity, so that the species involved are not usually polymorphic.

Some moths employ several distinct means of protection, one being held in reserve and used if another fails. Three examples, two being larvae and one an imago, will serve to illustrate this.

The larva of the Lobster Moth, *Stauropus fagi* L., Notodontidae, is one of the most curious found in Britain. It is brown in colour, the posterior end swollen and reflexed over the back, while the second and third pair of the ' true ' legs are greatly elongated. In the figure on Plate 19 these are folded, and in that position they are normally

Plate 13. POLYMORPHISM

1
CUMBERLAND

2
GLOUCESTERSHIRE

3
BERKSHIRE

4
SOMERSET

5
Male
BERKSHIRE

6
Male
N.W. YORKSHIRE

7
Female
BERKSHIRE

8
Male
SOMERSET

9
Female
SOMERSET

10
Male
SOMERSET

11
Female
SOMERSET

12
DEVON

13
DEVON

14
HEREFORD

1 and 2. Riband Wave, *Sterrha aversata:* 1 *remutata* form, 2 *aversata* form; 3 and 4. Dingy Footman, *Eilema griseola:* 3 typical, 4 var. *flava;* 5-7. Wood Tiger, *Parasemia plantaginis:* 5 and 7 typical, 6 var. *hospita:* 8-11. Silver Cloud, *Xylomyges conspicillaris;* 8 and 9 typical, 10 and 11 var. *melaleuca;* 12-14. Marbled Carpet, *Dysstroma truncata*

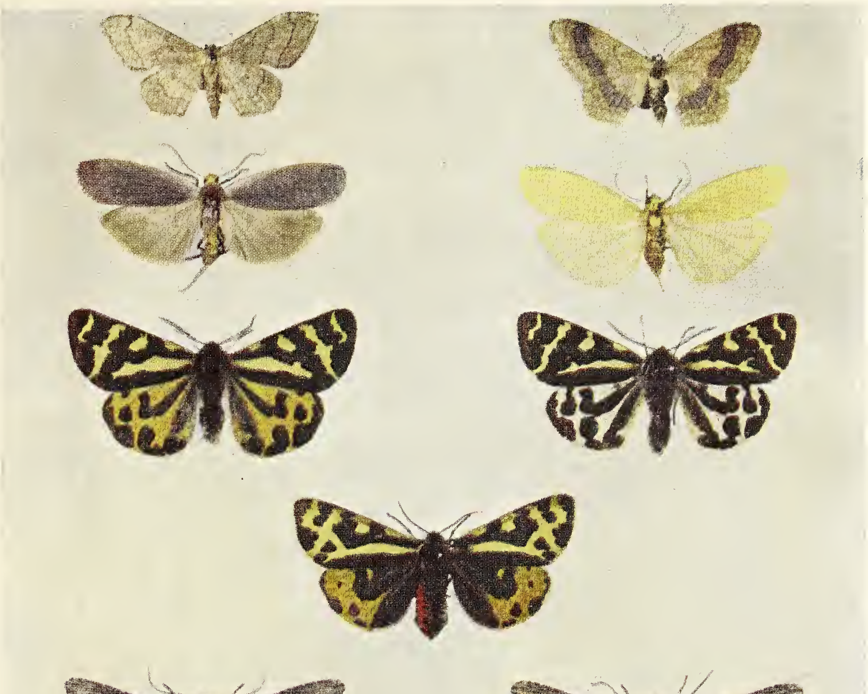


Plate 13

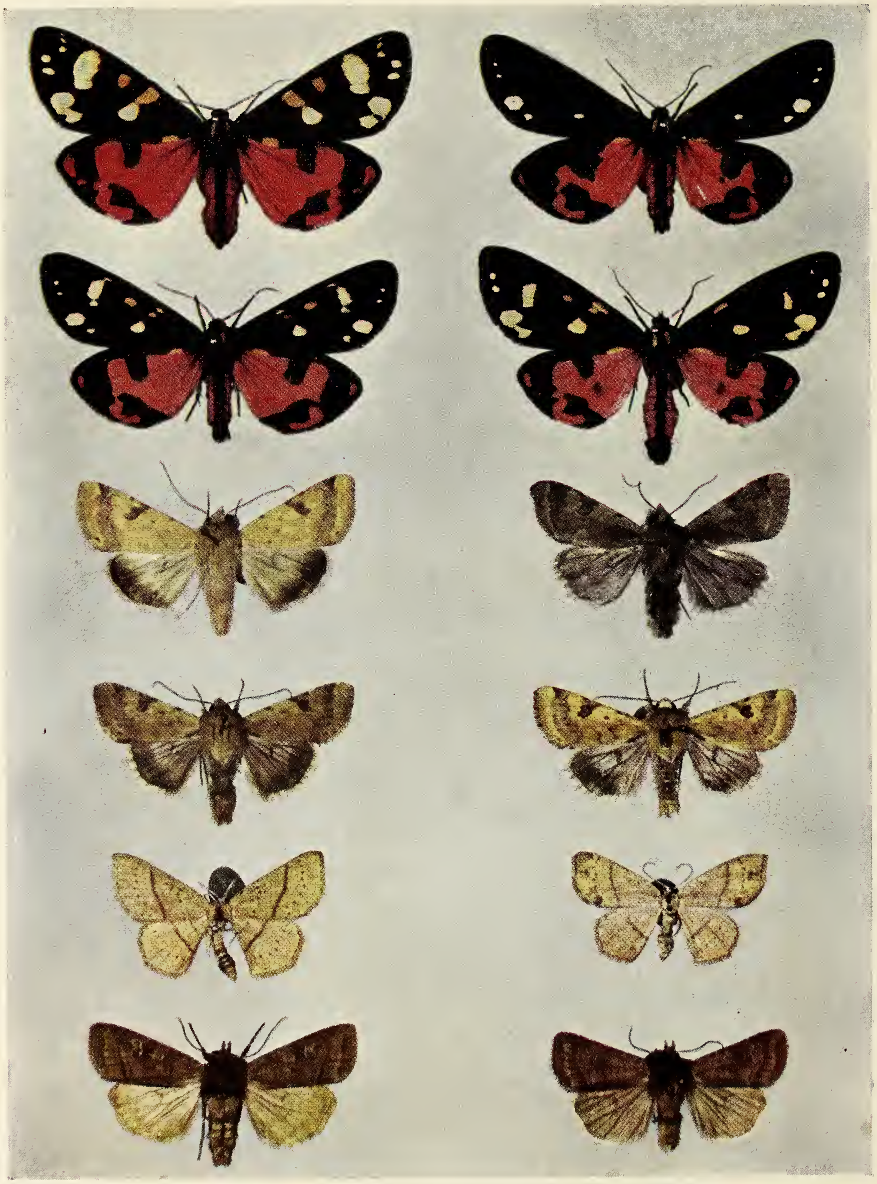


Plate 14

1
KETTLEWELL
EXPERIMENTS

2
KETTLEWELL
EXPERIMENTS

3
KETTLEWELL
EXPERIMENTS

4
KETTLEWELL
EXPERIMENTS

5
KETTLEWELL
EXPERIMENTS

6
KETTLEWELL
EXPERIMENTS

7
KETTLEWELL
EXPERIMENTS

8
KETTLEWELL
EXPERIMENTS

9
BERKSHIRE

10
BERKSHIRE

11
CAMBRIDGE

12
OXFORD

1-4. Scarlet Tiger, *Panaxia dominula,* temperature experiments: 1 typical, 2 homozygous variety, 3 and 4 heterozygous varieties; 5-8. Bordered Straw, *Heliothis peltigera,* temperature experiments; 9 and 10. Maiden's Blush, *Cosymbia punctaria;* 9 first brood, 10 second brood; 11 and 12. Small Square-Spot, *Diarsia rubi;* 11 first brood, 12 second brood carried; but if disturbed, the creature raises the front part of its body, bending back like a snake about to strike, at the same time extending the long fore-legs, the second pair of which begin to vibrate rapidly. It then somewhat resembles an ant or perhaps a spider, certainly not the caterpillar of a moth, and probably the deception often saves it. In addition, however, it has the power of ejecting formic acid of considerable strength from a gland opening below the front segment the thorax. Such a gland is widespread among the larvae of moths, but in this and some other species it is much enlarged. The discharge is certainly powerful enough, if well directed, to disable a small bird; furthermore, some of the acid is usually present on the surface of the body, probably making the insect unattractive not only to normal predators but also to the Ichneumons which might otherwise parasitise it.

The larva of the Puss Moth combines concealing and warning colouring in a remarkable way. It is at first black with two very long tails at the posterior end, which give it something the appearance of a withered leaf-stalk. As growth proceeds, it develops a complex colour-pattern. The body becomes apple-green with a purple diamond-shaped patch placed like a cloak upon the back. This patch is edged with white and the effect breaks up the shape of the larva, so that it is inconspicuous as it sits among the leaves of its food-plant: a method of protection by falsifying the creature's true outline which has already been described with reference to other species. If the Puss Moth larva be molested, however, it assumes an entirely different and terrifying appearance. A fold of skin round the head is inflated, producing a scarlet ' face ' on which are two black spots simulating eyes (Plate 22). At the same time each fork of the tail emits a long pinkish-red thread which lashes and wriggles. These threads, which give the impression of stings, are harmless but the creature itself is not so, for if further disturbed it emits strong formic acid in the manner of the Lobster Moth. Thus the Puss Moth manufactures formic acid as a larva, and softens its cocoon with strong caustic potash (page 101): a striking testimony to the efficiency of its physiological adaptations.

Finally, the use of multiple protective devices of another type may be illustrated by the Scarlet Tiger. When resting upon rushes, its chief food-plant the Comfrey, *Symphytum officinale*, or the flowers of Hemp Agrimony, *Eupatorium cannabinum*, on which it delights to settle, this gaudy insect is remarkably well concealed, for the dark bronze fore-wings marked with white spots are curiously suggestive of the interplay of light and shade (Plate 15). In warm weather it is a restive species easily disturbed, when the flicker of scarlet from the hind-wings acts as a flash colour. Nor is it easy to follow with the eye, rhythmically dipping and rising as it flies in bright sunshine. On a dull day when relatively inactive, it resorts to a typical warning technique. When molested the fore-wings are then thrust forward, displaying the brilliant red hind pair. At the same time two large drops of yellowish fluid are produced by glands behind the head. To me its flavour is slight but on the whole rather bitter; yet the reactions of the moth, which never attempts to fly once this procedure has been resorted to, strongly suggest that the secretion is repellent to its predators. Indeed I have several times seen it when flying, seized by a large dragonfly which, however, soon let it fall. Unfortunately I have never been able to find the specimen among the dense tangle of marsh plants in its habitat to discover whether or not it had been fatally injured. Dr. P. M. Sheppard informs me that he has once done so, and that it was but little damaged.

Certainly the most serious menace to which moths are exposed is that due to parasitism and disease. The parasites of butterflies have been discussed in the previous volume of this work (*Butterflies*, Chapter 6), and those of moths belong to the same groups and attack their victims in similar ways. On Plate IV, figure 1, is shown a larva of the Drinker, *Philudorina potatoria* L., Lasiocampidae, surrounded by larval parasites (Braconidae, see *Butterflies*, pages 109-11), one of which can be seen making its way through a hole which it has gnawed in the back of its host. They are escaping to pupate externally.

There can be no doubt, however, that virus disease constitutes the most serious menace to many of the Lepidoptera. The symptoms generally develop in late larval life. The affected individual becomes limp and passes liquid both from mouth and anus. Death follows in a day or two and the condition seems never to undergo a spontaneous cure. The excreta are highly infective and consequently crowding tends to spread an epidemic. Doubtless, therefore, this is a more serious hazard in gregarious than in solitary forms.

Populations of Lepidoptera overcome the ravages both of parasites and disease by the most fundamental of protective devices: that is to say, an adjustment between the number of eggs laid and the amount of elimination throughout life, so as to secure that each pair of insects shall, on the average, reproduce one pair but no more. Owing to the fluctuations in population-size to which so many moths are subject, this numerical relationship is, even in successful species, effective only when considered over several, sometimes many, generations. On the whole, however, the number of eggs produced is an indication of the dangers to which an insect's life is exposed and the efficiency of the protective devices by which it attempts to minimise them.

CHAPTER 8

INJURIOUS MOTHS

THE LEPIDOPTERA occupy a wide range of ecological habitats, yet few of the species are important pests, at any rate in Britain. The Small White Butterfly, *Pieris rapae* L., is the best known of these, and it has unfortunately become widespread in the temperate regions of the world, where it destroys cabbages and other Cruciferous vegetables on a scale which must be judged economically serious. The Large White, *P. brassicae* L., does so too, but it has not established itself so extensively outside Europe. Thus, travelling through New Zealand in 1951, I found the Small White causing considerable destruction to such crops, though it had only reached that country since the First World War. I was informed that the Large White was not known there, yet I myself saw a specimen flying about the railway track at Ohakune in the centre of the North Island. It will be interesting to know if that insect succeeds in establishing itself there, and the matter is likely to be of some consequence. The larva of the Cabbage Moth, *Mamestra brassicae* L., Caradrinidae (Plate 7, figure 3) also does some damage to cabbages in Britain and Continental Europe, but it is of negligible importance compared with these two butterflies.

Two species which are a notable menace in other lands have been unable to establish themselves permanently in Britain, though both of them occur sporadically here. The Gipsy Moth, *Lymantria dispar* L., (Plate 32, figure 3 male, 4 female), was accidentally introduced into the United States of America, where it has spread rapidly, causing immense damage in orchards and forests, so much so that it has been necessary to adopt control measures against it upon a vast and expensive scale; the method of trapping the males by means of a concentrated extract of the female's attractive scent has already been described in Chapter 1. In Europe this insect is adjusted to a Mediterranean climate. The original colony in these islands evidently subsisted precariously at the edge of its range, and the scattered specimens occurring since its extinction have shown no ability to re-establish the insect here (Chapter 14). It is this southern European race which found congenial conditions in some parts of North America. In Japan, however, exists a highly specialised form adapted to the almost Arctic climate of the most northerly island, Hokkaido. It has become a subspecies, giving rise to sexual abnormalities when crossed with specimens from Northern Hondo, the island which may be regarded as the Japanese 'mainland.'* Had individuals of this race rather than of Mediterranean origin been introduced into England, the history of the Gipsy Moth here might well have been very different.

The other dangerous pest which occurs only occasionally in these islands is the Scarce Bordered Straw, *Heliothis armigera* Hb., Caradrinidae (Plate xx, figure 9), see also Chapter 6. In some countries it does extensive damage, especially to corn and tomatoes, but it is an inhabitant of warmer climates than ours and it is never likely to become a menace here. The same may be said of the American Wainscot (page 82) and some other potentially injurious species among our Lepidoptera.

A few British moths cause damage by boring into the solid wood of trees. The only one common enough to constitute a pest is the Goat Moth, *Cossus cossus* L., Cossidae (Plate 5, figure 8), which especially attacks willow, ash and elm. The larva takes three or four years to reach maturity and, as it grows to a thickness of nearly half an inch (Plate 6, figure 1), the mines which it excavates in the trunk are usually very destructive: the result of their activity is shown in Plate vi, figure 1. This is quite a common insect in southern England, rarer but not unknown in the north of the country and in Scotland. The larva has a strong smell resembling that of a goat, and this clings to an infested tree. At the end of larval life it often leaves its burrow and wanders in search of a place where it can burrow into the earth to pupate.

An allied species, the Leopard Moth, *Zeuzera pyrina* L., lives as a larva in the stems or branches of a number of smaller trees and bushes, especially apple, and occasionally does a slight amount of damage in orchards, but is not frequent enough to be of much importance. Like the Goat Moth, it takes several years to reach maturity, but the larva does not leave its burrow for pupation. It is found only in the south and east of England, except for occasional records up to the northern Midlands.

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*The F_1 generation from a pairing between the two races consists of one sex only, owing to a sex-reversal either of males or females according to the direction of the cross. The sex-reversed females are, however, nearly inviable.

The Clearwing Moths, Sesiidae, are internal feeders, many of them in the branches or trunks of trees and bushes. The large Hornet Clearwing, *Sesia apiformis* Cl. (Plate 25, figure 4), bores holes up to the thickness of a lead pencil in poplars and aspens. Since it mines the wood at the base of the trunk it sometimes causes the taller trees to break off near the ground. The pupa is enclosed in a cocoon of gnawed wood constructed near the mouth of one of the mines, from which the broken remains of the pupa-case may be seen protruding after the emergence of the moth (Plate xvii, figure 3). The larva of the Currant Clearwing, *Aegeria tipuliformis* Cl., lives in the branches of both black and red currants, feeding on the pith. Though it does some damage to these plants, it is not common enough to constitute a serious threat to growers.

Two other British moths are, however, quite important pests both of currants and gooseberries, stripping them of their leaves. The Currant Moth, *Abraxas grossulariata* L., Selidosemidae (Plate 11, figure 6), is abundant throughout Britain. Both the larva (Plate vi, figure 2) and the pupa (Plate ix, figure 2) are conspicuous and warningly coloured (Chapter 7). These larvae often swarm also on the imported *Euonymus japonicus.* Their natural food-plants seem principally to be hawthorn and sloe and, in the north, heath and ling. The V-moth, *Itama wauaria* L., of the same family (Plate 5, figure 6), is almost as injurious to bush fruit as is the Currant Moth. The larva is cryptically coloured, being of a greenish hue.

It is probable that to the farmer the most serious pest among the British Lepidoptera is the Turnip Moth, *Agrotis segetum* Schiff., Caradrinidae (Plate 5, figure 5). In some years this is immensely abundant, the larvae destroying turnips and swedes in great numbers. They bore their way into the bulbs and excavate large cavities in them. This is an extremely variable species and the females are on the average darker than the males. The imagines fly in June and there is a partial second generation in the autumn, consisting of moths rather smaller and paler than the summer form.

The remarkably wide range and abundance of some of the species with flightless females, which depend upon their larvae for dispersal, has already been discussed (Chapter 6). Two at least of such moths are common enough to cause extensive damage by defoliating trees. The Winter Moth, *Operophtera brumata* L., Hydriomenidae (Plate 5, figure 3 female, 4 male), attacks both forest and fruit trees. The larva pupates among litter on the ground, so the almost wingless females are often caught by placing bands of sticky substance round the trunks of apple trees. These trap them when they emerge in the winter and climb upwards to lay their eggs upon the branches. The small green caterpillars feed during May and June. They are then preyed upon by the larva of the Dun-bar Moth, *Cosmia trapezina* L., Caradrinidae (Plate 7, figure 1), which hunts them down and devours them. This species seems to have become almost completely carnivorous.

The larva of the Mottled Umber, *Erannis defoliaria* Cl., Selidosemidae, shown in its characteristic looping attitude on Plate 7, figure 2, feeds principally upon forest trees. It occurs in immense abundance, and together with that of the Winter Moth and the Green Tortrix, *Tortrix viridana* L., is largely responsible for defoliating oaks in late May. No sooner are these and other trees in full leaf than they are in some years reduced once more to the condition of winter by vast hordes of these caterpillars, whose frass, falling upon the undergrowth in a continuous shower, makes a distinct pattering noise in the forest. The growth of trees so affected is checked for that year, and the devastation may affect woods over a vast area. The Mottled Umber is another of the species which has achieved an extremely wide range although the female is flightless (Plate XVIII, figure 1 male, 2 female).

The Common Swift, *Hepialus lupulinus* L., Hepialidae, feeds in the larval stage upon the roots of grasses and occasionally does a small amount of damage to lawns and meadows (Plate XVI the larva and VII the imago). However, its effects are insignificant compared with those of the Antler Moth, *Charaeas graminis* L., Caradrinidae (Plate 5, figure 7), the larva of which sometimes appears in such immense numbers as to produce an effect like a plague of locusts. Every blade of grass is eaten, and in Westmorland I have seen from afar the brown area of destruction advancing daily farther down the mountain-sides. Flocks of rooks and other birds arrive to prey on them, but they do not reduce their numbers perceptibly. The serious effects of this insect seem restricted to Scotland and the north of England, and there principally to hilly and mountainous country.

In the last instance it might be worthwhile to trap the moths on a large scale after one of these outbreaks. They then fly in myriads in late summer and could be caught by some of the new high-powered mercury-vapour lamps (Chapter 1). This might help to avert a repetition of the epidemic the following year. Such methods are perhaps applicable to other instances in which a moth has done extensive local damage. I do not think, however, that many species in addition to the Antler are very suitable for such treatment, which must be carefully carried out to avoid the destruction of the other insects which are also attracted. On the whole, our injurious moths do not constitute so serious a problem as to merit extensive or costly methods of control.

CHAPTER 9

GEOGRAPHICAL DISTRIBUTION

Localised Moths

There is always a reason why any species of moth lives in a particular locality. It may be simple or very recondite but, simple or complex, it is rarely known. Yet such information is much more often available in some other groups of organisms. We do know something of the ecological and physiological preferences of fresh-water Crustacea; the plankton recorder developed by A. C. Hardy is year by year accumulating data on the reasons why certain fish are found at a given place at a particular time; the ecological and physiological requirements of some annelids and of ' wire-worm ' larvae have been worked out in detail; so, to consider a more circumscribed problem, has the territory system in birds. Such investigations have proceeded still further in plants: for plant ecology is at a more advanced stage, and is potentially much less difficult, than is animal ecology. But when we turn to that group which has more than any other attracted the attention of collectors, the Lepidoptera, our ignorance of the facts affecting the distribution of the species is extreme, nor is this altogether unexpected. Many collectors are good naturalists, but the very nature of their hobby tends to make them think " where " rather than " why " an insect is to be found in a given area. The ornithologist is free to devote himself to observing the habits and behaviour of birds in the countryside, since he is seldom a collector: for the nest-robber who collects birds' eggs can rarely claim to be an ornithologist or a naturalist. On the other hand, the man who forms a collection of moths spends much of his time in adding to his series and amassing varieties, too often as mere curios, and has the less to give to observation and experiment.

In general terms, organisms can solve the problem of their distribution in one of two ways. They may fit themselves to tolerate a wide range of environment or they may become adjusted with increasing perfection to one particular type of habitat: that is to say, they may be either *euryplastic* or *stenoplastic*. In addition, the euryplastic species may be 'buffered' in a high degree against the changing conditions they encounter or they may accommodate themselves to them by minor variation, so giving rise to clines and geographical races; and to such insects polymorphism is a valuable asset.

As already explained in *Butterflies*, pp. 149-151, species can usually survive at the extreme edge of their range only by becoming stenoplastic and adapting themselves closely to some special type of habitat, one which may be very different from that which they normally occupy. The adaptations involved will primarily be ecological, and the genes concerned may or may not affect visible characteristics such as the colour-pattern. For instance, in Britain the Feathered Ear, *Pachetra sagittigera* Hufn., Caradrinidae, is, except for occasional vagrants, restricted to chalk-downs and only to those small areas of them situated between Ashford and Wye in Kent, near Reigate, and at a few places in Wiltshire. It has a wide distribution abroad and is by no means confined to this type of habitat there, but the specimens which are so localised in this country are somewhat whiter than the European form. On the other hand, the Grey Moth, *Hadena caesia* Schiff., Caradrinidae (Plate 26, figure 4), is able to maintain itself in these islands only on the rocky coasts of the Isle of Man, the Island of Canna in the Inner Hebrides, and Southern Ireland. In Europe it is widespread and not restricted to coastal districts; but our own specialised race, *manani*, has come to differ in coloration as well as ecology from that living elsewhere, being of a less bluish shade.

The Deal Footman, *Eilema pallifrons* Zell., Arctiidae, is an extremely localised insect in this country. It exists as a distinct subspecies, *pygmaeola* (Plate 26, figure 15), always associated with sandhills, in the neighbourhood of Deal in Kent and at a few places on the Norfolk coast. This occurs nowhere else in Europe save in Holland, though the specimens are larger there than in England. However, Kettlewell has discovered that a form indistinguishable from the true *pallifrons* exists at Lydd, Kent. This is 40 miles from Deal, and there are no sandhills there. *E. pallifrons* differs from the subspecies *pygmaeola* in being larger, of a yellower tint with a black shading at the base of the hind wings, and in possessing bright yellow thoracic tufts.

The fact that those moths which are isolated in exceptional localities in Britain sometimes differ recognisably from their normal Continental forms prepares us to find that some have become specifically distinct in these islands. It may also be that a colony adjusted to unusual conditions here has survived when the insect has become extinct elsewhere. Until the special circumstances involved are considered, it may appear surprising that exceedingly few instances are known of moths restricted to the British Isles. However, it must be remembered that the climate of England had only reached sub-arctic conditions after the last of the four Pleistocene Ice Ages between 8,000 and 9,000 B.C. Consequently the time for such evolutionary changes to take place has been extremely short (Chapter 11).

The Small Autumnal Carpet, *Oporinia filigrammaria* H.-.S., Hydriomenidae, appears to be a purely British insect unknown elsewhere. So does Fenn's Wainscot *Arenostola brevilinea* Fenn (Plate 26, figure 8), Caradrinidae. However, it is just possible that this still awaits discovery in Central Europe, where the moth fauna is far less thoroughly known than here. In fact, the independent evolution of British moths is illustrated rather by the existence in these islands of subspecies or geographical races (Chapter 12) than of species that are unique.

Before considering some of the moths that are characteristic of different types of habitat, it is desirable briefly to discuss a few instances of extreme localisation. As will become apparent, several of them are doubtless to be interpreted as species with specialised requirements at the edge of their range.

I should like here once more to draw attention to the construction of this book. As is appropriate in this Series, it is concerned with *principles*, of which the species mentioned are merely selected examples. It is not intended that they should comprise all those known to inhabit the particular types of country that are discussed, or that they should constitute exhaustive lists of those with greatly restricted habitats, unusual food-requirements or any other characteristics which are related to their geographical distribution in these islands.

There are but few British moths whose distribution is rigorously limited because they feed upon some rare plant and have not been able to accustom themselves to an alternative diet. The larva of the Netted Carpet, *Eustroma reticulata*, Schiff. (Plate 26, figure 1), Hydriomenidae, feeds only on Yellow Balsam, *Impatiens noli-me-tangere*, and consequently the moth is wholly confined to the places where it grows which, in this country, are extremely restricted: the borders of Westmorland and Lancashire, and North Wales. The Scarce Hook-tip, *Drepana harpagula* Esp. (Plate 26, figure 9) Drepanidae, though omnivorous abroad, in England lives only upon the Small-leaved Lime, *Tilia cordata*. It is said that it will readily eat other species of lime, but that they are poisonous to it. This, though a native, is not a common tree in Britain, but the Scarce Hook-tip is found in only one of its localities, Leigh Woods near Bristol. This probably constitutes the most extensive area of *Tilia cordata* in Britain, but it is certainly surprising that the moth appears to be absolutely localised to this place. Leigh Woods crown the southern side of the Avon Gorge, and the site is an exceptional one. Presumably it provides conditions in addition to this moth's exacting food-requirements which enable the insect to live far beyond its normal range.

Many other species intensely localised in Britain are not restricted by any such obvious limitation as that imposed by their food-plant. Though the factors which control them are generally unknown, it will be useful to give a few examples, since they would provide admirable material for detailed ecological studies, both in the field and the laboratory, which might reveal the nature of their special habitat-preferences. Work of this kind should include an investigation of the microclimate, superficial geology, and plant and animal ecology of their favourite haunts. The species should also be bred under controlled conditions, the components of which could then be studied and their effects compared.

The Lewes Wave, *Scopula immorata* L. (Plate 26, figure 2), Sterrhidae, is in Britain restricted to heathy country in the neighbourhood of Lewes in Sussex, where the larva feeds on Ling, *Calluna vulgaris*, although it has a wide distribution through Europe and Asia. It is likely that a locality of this kind is of an exceptional type, the ecological features of which would be well worth investigation. Another mysteriously restricted species, whose chief locality is in the same neighbourhood but on alkaline soil, is the Scarce Forester, *Procris globulariae* Hb. (Plate 26, figure 11 male, 12 female), Zygaenidae. This occurs in a few other stations in the same county and in Kent. Also in Wiltshire, where among miles of chalk-down supporting the closely allied *P. geryon* Hb., it is found in two valleys only. Its food-plants are the common Knapweeds *Centaurea nigra* and *C. scabiosa*.

A very similar problem is raised by the habitat of the Silky Wave, *Sterrha dilutaria* Hb. (Plate 26, figure 7). Apparently its requirements could be met in a great variety of places and over wide areas in the southern part of England, as they are abroad, for it is found among bushes and low vegetation on rough ground and downlands, where it feeds upon Rock-Rose, *Helianthemum.* Yet its distribution is extremely restricted, to a few small areas of this type in Buckinghamshire, Dorset, Norfolk and Wales. Its best-known locality, however, is on the northern slopes of the Avon Gorge at Bristol which, strangely enough, therefore divides the haunt of this species from the unique locality of the Scarce Hook-tip on the other side. This little moth has a decidedly southern distribution in Europe and evidently maintains itself here with difficulty.

Several species exist in isolated colonies in North Wales, two of them nowhere else in Britain. Penmaenmawr and a few neighbouring mountains are the only known habitats of Ashworth's Rustic, *Amathes ashworthii* Dbl. (Plate 26, figure 3), Caradrinidae. However, it may well be more widespread than is at present suspected.* Central Wales is very mountainous and is largely unexplored entomologically. Indeed, it has always constituted a formidable barrier to travel; so much so that the Celtic populations of North and South Wales have remained significantly distinct, as indicated by their blood-groups. If, as seems reasonably well established, this insect is specifically different from *A. candelarum*, it provides a further instance of a purely British moth. The other species restricted to approximately the same distribution, but to lower elevations, is Weaver's Wave, *Sterrha eburnata* Wocke (Plate 26, figure 5), which feeds principally upon Ling, *Calluna*, so that its stringent requirements are not dictated by its diet. It is fairly widespread in Central and Southern Europe.

Several coastal moths are quite mysteriously localised, and to an extreme degree. An example is provided by the Isle of Wight Wave, *Sterrha humiliata* Hufn. (Plate 26, figure 6), which is found in one place only on the cliffs of the Isle of Wight. Ths species is inconspicuous and easily confused with the closely related Dwarf Cream Wave, *S. fuscovenosa* Goeze, from which it is to be distinguished by a reddish stripe along the costa of the fore-wings and by other less well marked characteristics. Consequently it may have been overlooked in one or two areas, but it must certainly be extremely localised here, for it has rather a southern distribution in Europe. On the other hand, it is hardly likely that colonies of the Portland Ribbon Wave, *Sterrha degeneraria* Hb. (Plate 26, figure 16), have passed unnoticed, at least in southern England, for this is a fairly distinctive insect. It is confined to the Isle of Portland and the coast near Torquay in Devon. Its food-plant in Britain seems to be unknown. When discovered it may possibly throw some light on its distribution here, though that does not seem probable. This is another of those curious instances in which a species is restricted to the coast in this country though its habitats in Central Europe are entirely different. There it is found far inland and occurs widely in France, Central Germany, Austria and other places, but not in Northern Europe. Consequently, like several of the other moths quoted, this is probably a species surviving on the edge of its range only because it has adapted itself closely to special conditions, and it doubtless requires more warmth and sunshine than is usual in England.

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*Dr. Kettlewell informs me that he possesses a specimen of this moth from Carnforth, Lancashire, which looks different from other forms. It may well be that a small colony has evolved in isolation in that district, having colonized it from an area now submerged by the Irish Sea (see chapter 11).

New or Little-known Species

A few native species of extremely localised distribution and rather skulking habit must await discovery in Britain. Thus very few specimens of the Brighton Wainscot, *Oria musculosa* Hb., Caradrinidae (Plate 3, figure 2), had been recorded here until Drs. Cockayne and Kettlewell determined its true habitat in 1938. They found it abundantly in wheat-fields near Salisbury. It rests on the ears of corn by day and takes to the wing at dusk. When disturbed, as it is when a field is reaped, it flies out rapidly and usually hides itself in the nearest sheaf. The larva feeds upon young shoots of corn in the spring. Now that its habits are to some extent understood, it is known that this moth, so long thought to be merely a rare immigrant, is widely established in Wiltshire and Hampshire, and it will doubtless be found in other areas.

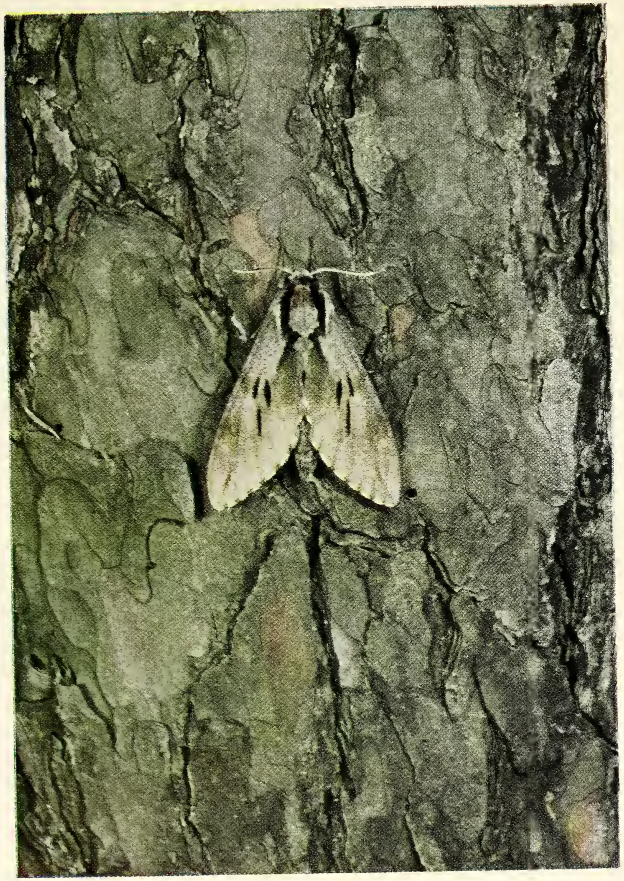
A more questionable example is provided by *Sedinia buettneri* Her., Caradrinidae (Plate 29, figure 1), which was discovered in a single marsh near Freshwater, Isle of Wight, in 1945. It is quite common there, but no specimen had previously been reported in Britain. This insect has an extensive distribution in Central Europe and it is probable that the Freshwater colony was established by migrant specimens, for the locality only became a marsh fifty years ago. On the other hand, it is conceivably an endemic species which has spread from some other area where it has not yet been detected, for it could be easily overlooked.

The Waved Black, *Parascotia fuliginaria* L., Plusiidae, was until recently an insect of the greatest rarity, obscure and little known on the Continent as in England. Most of the British specimens had been taken in London, about the City or in the docks, and the larvae had on a few occasions been found feeding on a fungus growing on the rotting wood of old buildings or of wharves. However, in 1932 larvae were discovered in Surrey, and the species is now known to be widespread both in that county and in East Berkshire. It had been overlooked owing to its unusual and secretive habits.

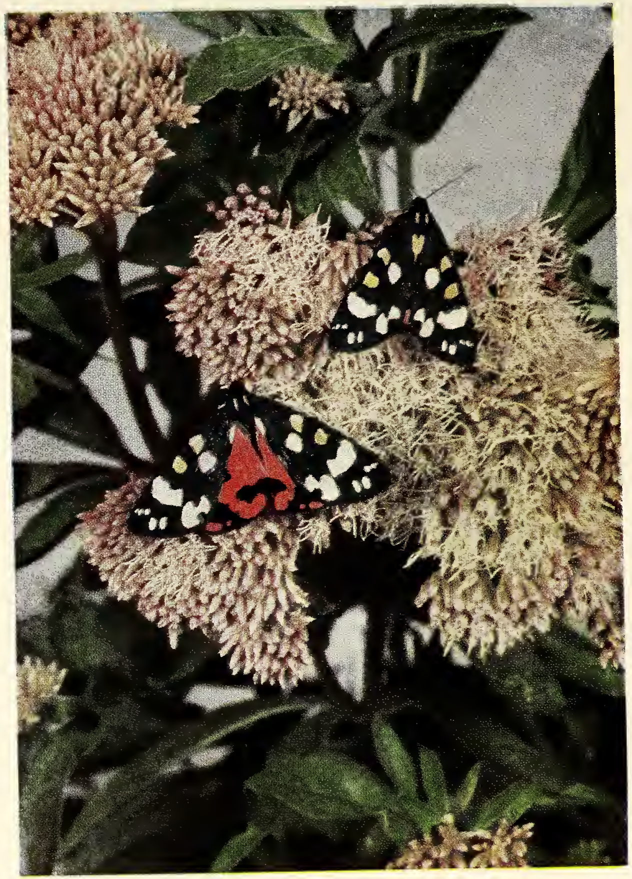
Normally the larvae feed on fungi* growing on rotting logs in damp situations. Now that their ecology is understood, they are not hard to find in their appropriate localities. Mr. R. F. Bretherton and I, during one afternoon's search, easily obtained the specimens shown on Plate 4, from which the imago illustrated on the same plate was reared. The pupae are housed in a swinging hammock-like cocoon composed of silk and pieces of the fungus (Plate XI), and the skulking behaviour of the perfect insects, already mentioned in Chapter 7, ensures that these are seldom seen.

There must be other species which are rare only because their habits are not understood. The Dusky Clearwing, *Sciapteron tabaniformis* Rot., Sesiidae (Plate 29, figure 10), is probably one of them. It is accounted a very great rarity and less than two dozen specimens have been recorded from Britain, though they have occurred over a long period of time, and once or twice the larva has been found here feeding under the bark of poplar trees. The moth has several times been taken when a tall poplar has been felled, so that as an imago it may be an inhabitant of the tree-tops. A number of other species could be quoted in this connection, but one more example must suffice. The Three-Humped, *Notodonta tritophus* Fab. (Plate 29, figure 7), Notodontidae, belongs to a group of moths notoriously difficult to find in the imaginal state unless attracted by light, which this particular species seems not to be. The larva feeds on poplar and if it tends to frequent the higher branches may very seldom be found, though it is extremely characteristic when seen. Less than a dozen specimens

*The species are said to be *Polysticus versicolor, Daldinia concentra* and *Polyporus schweinitzii.*

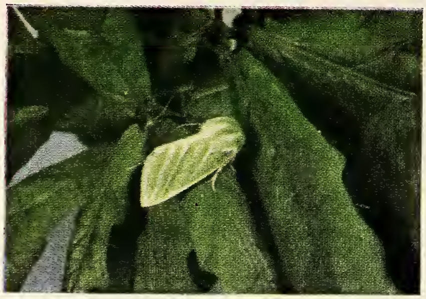


1. Pine Hawk, *Hyloicus pinastri* × $\frac{3}{4}$

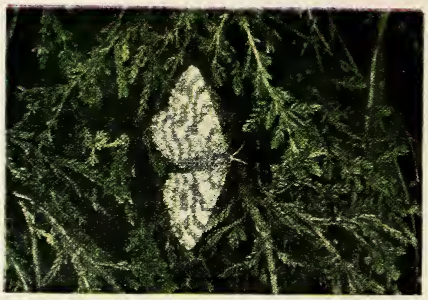


2. Scarlet Tiger, *Panaxia dominula*

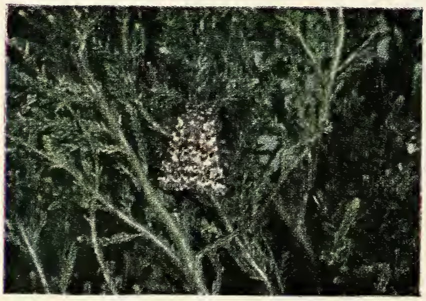
Plate 15. Warning Colours and Cryptic Colours



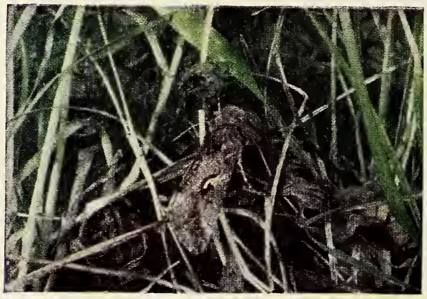
1. Green Silverlines, *Bena prasinana*



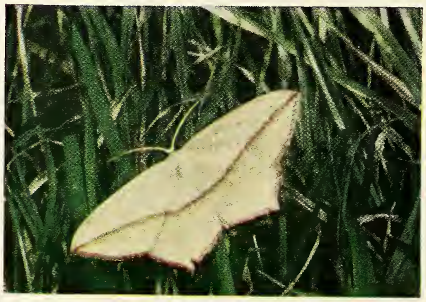
2. Common Heath, *Ematurgia atomaria*, female



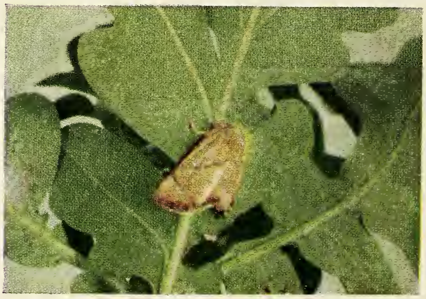
3. Beautiful Yellow Underwing, *Anarta myrtilli*



4. Silver Y, *Plusia gamma*



5. Blood Vein, *Calothysanis amata*



6. Festoon, *Cochlidion avellana*

Plate 16. CRYPTIC COLOUR-PATTERNS
(Blood Vein × 1¼)

of the insect have been taken in Britain, but their distribution has been widely scattered and about half of them have been larvae. On the whole it is likely that the Three-Humped is distributed at a low density over a wide area in southern England, that its habits here are not understood and that they are in any event of a kind to make it difficult to capture.

It is interesting to note that an instance precisely corresponding to the two here mentioned, but now elucidated, is provided by the Orange-tailed Clearwing, *Aegeria andreniformis* Laspeyres, Sesiidae. Up to 1906 this was as rare as either of them. It was then discovered that the larva lives in mines excavated in shoots of the Wayfaring Tree, *Viburnum lantana*, and that the species is not only widespread but abundant where its food-plant grows: but no way of attracting or finding the imago has been discovered, except by "assembling" the males to a virgin female, and very few of the perfect insects have otherwise been seen wild.

Two of the reasons why some moths have been overlooked in Britain have so far been mentioned. Other causes may briefly be considered with the help of a few examples selected from a considerable number of species. In certain instances, a moth occupies a type of habitat seldom investigated, though situated in a part of the country which may be fairly well known entomologically. *Lampropteryx otregiata* Metcalfe, Hydriomenidae, is shown on Plate 29, figure 9, where it is compared with the well known Water Carpet, *L. suffumata* Schiff. (figure 8), to which it is closely related. It was first reported in 1917 as having been found in the wettest and darkest parts of dense woods in Devon and Cornwall. The difficulties of capturing it are increased by the fact that it does not fly until well after dark.

Quite a number of Lepidoptera have until recent years escaped recognition because they have been confused with some other species. Indeed even a new butterfly, *Colias calida* Vty., has been added to the British list since the first volume of this Series was published. It had not been distinguished from the Pale Clouded Yellow, *C. hyale*, which it resembles to an extreme degree as an imago though less as a larva. This indeed raises the possibility that two species may sometimes be confused because apparently identical as imagines though easily separated in the early stages. An illustration of this situation is provided by the Grey Dagger, *Apatele psi* L. (Plate 17, figure 16 larva, figure 14 imago) and the Dark Dagger, *A. tridens Schiff* (Plate 17, figure 15 larva, figure 13 imago), Caradrinidae. They have long been distinguished owing to their conspicuous larvae, but there may be other such instances not yet recognised. It should be remarked however, that the colour-patterns of larvae are on the whole much less diagnostic than those of the perfect insects.

Logically one might expect the existence of pairs of distinct species which, though completely sterile with one another or producing sterile offspring, cannot be separated by their appearance at any stage and are kept apart owing to differences in attractive scent and through the absence of interbreeding which has arisen thereby. Their independent evolution would have to take place in geographical isolation, though they might subsequently spread and overlap each other's territory, as so often happens during the extension of range which follows an Ice Age. Instances of the kind are known in other organisms (for example, *Drosophila pseudo-obscura* and *D. persimilis*, and the Tree-creepers *Certhia familiaris* and *C. brachydactyla*). One wonders whether they do not occur or have not been recognised in the Lepidoptera.

The two species of the Treble-bar, *Anaitis plagiata* L., and *A. efformata* Gu., Hydriomenidae, were only distinguished from one another in this country and clearly established as distinct species in 1923. So too, *Oporinia christyi*, Prout. (Plate XII, figure 10), Hydriomenidae, was long confused with the ordinary November Moth, *O. dilutata*, Schiff. (figure 8), from which it can be separated by its genitalia, its paler coloration and its slightly different markings.

On Plate 29 are illustrated two forms of the Five-spot Burnet, *Zygaena trifolii* Esp., which have been thought distinct species, though the matter is still in doubt. The larger race is found in marshes (figure 5), spins its cocoon fully exposed high up on grasses and emerges later in the year. The smaller one occurs on downland (figure 6), appears on the whole earlier and evidently constructs its cocoon in quite a different situation, out of sight, though in what position does not seem to be known. The genitalia are but little guide to specific identity in the Zygaenidae, and the status of these two forms should be studied genetically and cytologically. We require to know whether or not their chromosome-numbers are the same, if their chromosomes pair regularly and whether there is any tendency for the female offspring (page 42) to be relatively rare or sterile when they are crossed.

Most countries contain large areas that are very little studied entomologically. This is less true of England than of any other, though Holland and Belgium may be almost equally well worked. In Wales, Scotland and Ireland the situation is very different, and the discovery of moths new to these islands or heretofore of great rarity may with some confidence be expected from a more thorough investigation of their entomology. When it is remembered that a butterfly new to Scotland (*Carterocephalus palaemon* Pall.) was only discovered as recently as 1942 it will be realised that this is no extravagant claim. I have reason to believe that the Pease-blossom, *Periphanes delphinii* L., Caradrinidae, is to be found in Wales. It is so rare in Britain as to be virtually unknown. The Oban Burnet, *Zygaena achilleae* Esp. (Plate 27, figure 9), was not recognised in Scotland until the beginning of this century. When it is considered how sparsely moth-collecting has been carried out over the great area of the Highlands, it would not be surprising if striking new discoveries were to be made there.

I would like to draw attention to one aspect of ‘ collecting ’ which has greatly held back the advance of entomology. That is the tendency to frequent well-known localities, such as Rannoch in Perthshire or Aviemore in Inverness, instead of breaking new ground. I am fully alive to the value of studying an area or a particular colony of insects intensively, perhaps for many years, in order to elucidate some ecological or evolutionary problem : I have done so myself. But the tendency to go to some locality celebrated for rare insects merely to find them, is pernicious, if we gain no fresh information by this means. It is noteworthy that the experienced collector who visits sites entomologically unknown, of which there are plenty in Scotland, nearly always finds something unexpected and interesting.

What is true for Scotland or Wales applies with still greater force to Ireland. The entomological resources of that island have hardly yet been assessed. It is true that in number of species its fauna is uniformly poor, but it is of extreme interest owing to the survival, especially in the south-west, of forms destroyed by the fourth Pleistocene Ice Age in Britain. A few examples of the remarkable discoveries lately made there by moth-collectors will be discussed in Chapter 11, for until recently such insects have not so much been overlooked as unsought. The appendix added to the end of both volumes of the new edition of R. South's well-known work, *The Moths of the British Isles*, gives a list of most of the species which have been found since it was first published in 1907, together with brief accounts of those which

Plate XIII. Hybrids

1
Female
KENT

2
Male
(EXPERIMENTAL MATERIAL)

3
Male
RANNOCH

4
Male
CARNARVON

5
Female
RANNOCH

6
Male
(EXPERIMENTAL MATERIAL)

7
Female
CARNARVON

8
Male
LONDON

9
Female
LONDON

10
Male
(EXPERIMENTAL MATERIAL)

11
Female
(EXPERIMENTAL MATERIAL)

12
Male
(EXPERIMENTAL MATERIAL)

13
Female
(EXPERIMENTAL MATERIAL)

---

1. Purple Thorn, *Selenia tetralunaris;* 2. *Selenia bilunaria* × *S. tetralunaris;* 3 and 5. Rannoch Brindled Beauty, *Poecilopsis lapponaria;* 4 and 7. Belted Beauty, *Nyssia zonaria;* 6. *P. lapponaria* × *N. zonaria;* 8 and 9. Brindled Beauty, *Lycia hirtaria;* 10 and 11. *P. lapponaria* × *L. hirtaria;* 12 and 13. *N. zonaria* × *L. hirtaria*

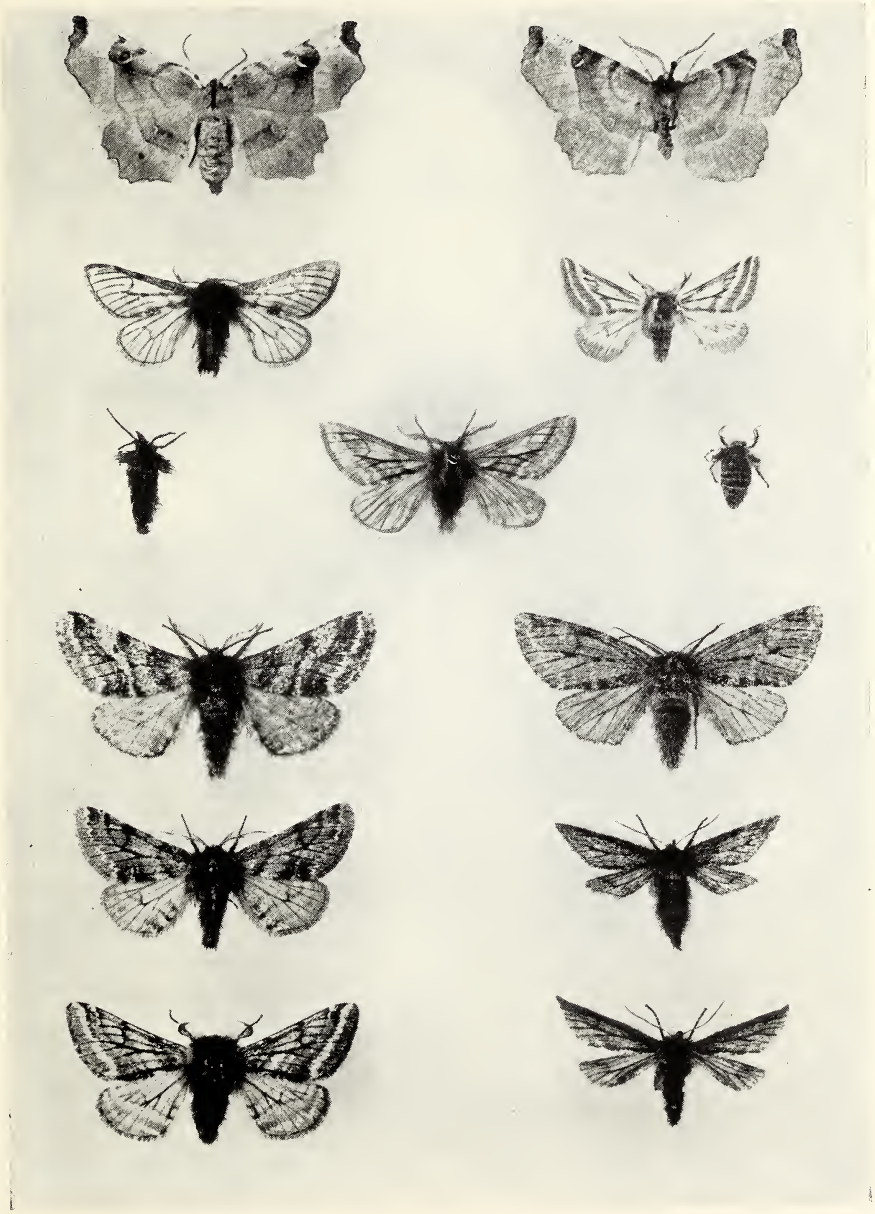


Plate XIII

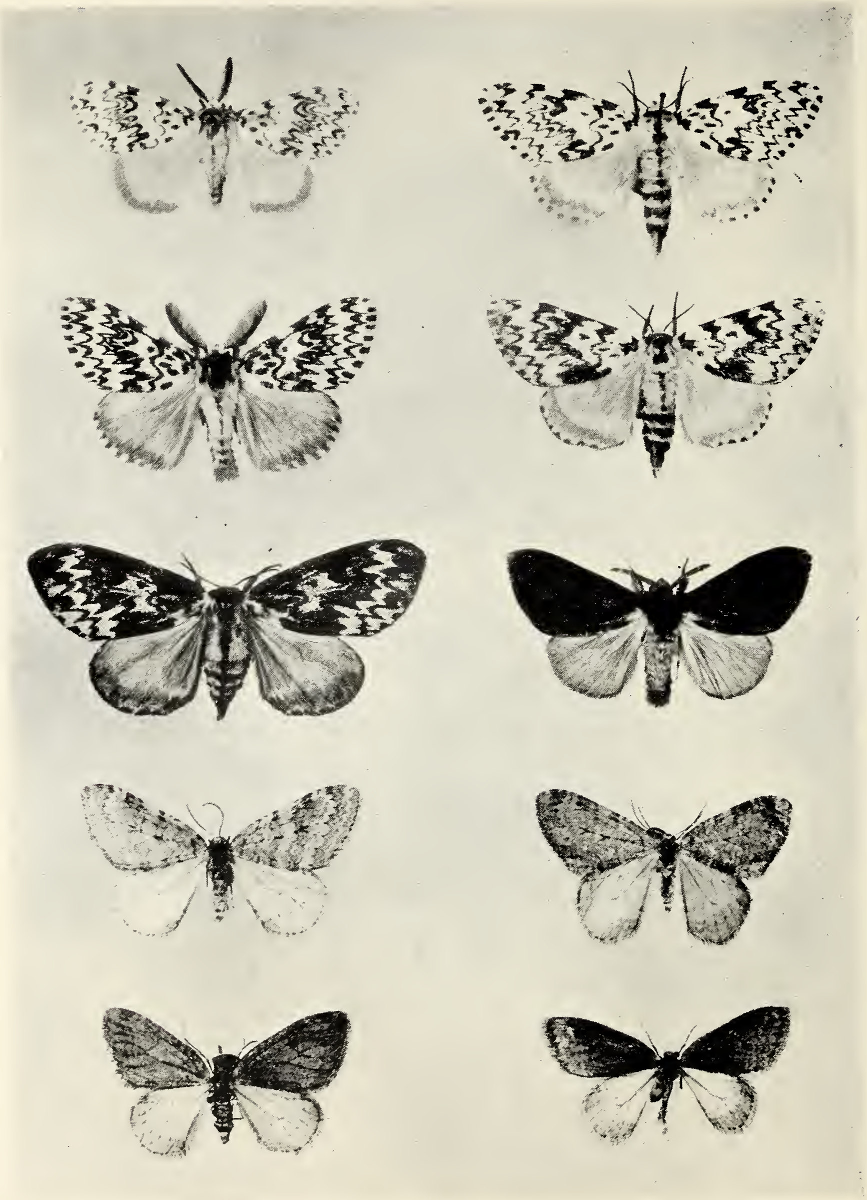


Plate XIV

1
Male
NEW FOREST

2
Female
NEW FOREST

3
Male
SURREY

4
Female
'ENGLAND'

5
Female
SUSSEX

6
Male
NEW FOREST

7
CUMBERLAND

8
CUMBERLAND

9
YORKSHIRE

10
KENT

1-6. Black Arches, *Lymantria monacha;* 7-10. November Moth, *Oporinia dilutata* have proved much commoner than at one time supposed. Most of these have never been figured, or at all fully described, in any easily accessible publication, and there is a great need for such information. I had originally intended to supply it in this book but the cost has proved prohibitive. It must now be done in some text-book of British Lepidoptera rather than in a work of this kind, the purpose of which is to use that Order to illustrate some of the principles of natural history.

CHAPTER 10

TYPES OF HABITAT

The Sea Shore

Large numbers of moths are adapted more or less strictly to life on or near the sea shore. The adjustments which fit them to such conditions are occasionally obvious but more often unknown, and some of these species are by no means confined to a coastal habitat outside Britain. The distribution of a few such insects is determined by the fact that they feed exclusively upon plants that grow near the sea. For example, the larva of the Scarce Pug, *Eupithecia extensaria*, Freyer, Hydriomenidae, eats only the Sea Wormwood *Artemisia maritima*, which is never found but on the shore and in salt marshes. But this moth must in addition be limited by other factors which confine it to that part of the coast which lies between the Thames and the Humber. This and the country behind it is the only region of Britain where the climate approaches the dry ' Continental ' type, and such conditions or some outcome of them may well supply an environment necessary for the moth. The food-plants of Barrett's Marbled Coronet, *Hadena barrettii* Ddl., Caradrinidae, are Sea Campion, *Silene maritima*, and Rock Spurry, *Spergularia marginata*, and both are confined to rocky, sandy or shingly shores. The Sand Dart, *Agrotis ripae* Hb., Caradrinidae, can eat a somewhat wider range of species, but they are all restricted to sandy coasts (Sea Holly, *Eryngium maritimum*: Sea Rocket, *Cakile maritima*, and a number of others). Also, to take an instance from a very different group of moths, the larva of the Thrift Clearwing, *Aegeria muscaeformis*, View., Sesiidae, feeds only on the roots of Thrift, *Armeria maritima*, a plant almost confined to the neighbourhood of the sea shore, yet growing also in a few places on the tops of mountains where the Thrift Clearwing is not known to follow it; though this minute inconspicuous insect might well do so without having been detected in such places. However, its wide distribution along the British coasts is a clear reflection of its food requirements. A considerable list of moths could be drawn up which feed only upon shore plants: the Shore Wainscot, *Leucania litoralis* Curtis (Plate 17, figure 8), upon Marram Grass, *Ammophila*, and the Lyme Grass Moth, *Arenostola elymi* Treits, both Caradrinidae, upon the plant, *Elymus*, after which it is named, may be quoted among instances not so far mentioned.

Some moths are limited to the coast by reason of adaptations which they have acquired to this type of habitat, though these are unconnected with their food. As already explained (Chapter 7), the larva of the Portland Moth, *Actebia praecox* L., Caradrinidae, lives by day in a vertical tunnel in the sand and is appropriately coloured to match the sandy surface over which it crawls to reach its food (Plate 6, figure 2 larva ; Plate 1, figure 2 imago). This consists principally of plants which can grow equally well inland: grasses, dwarf sallow, chickweed and others : although it will eat Sea Wormwood. However, the method of larval concealment tends to confine this moth to the shore, though a curious isolated colony of it occurs on a common near Birmingham where the very sandy soil provides a moderately appropriate habitat for it. A certain number of species seem to be restricted principally to sandhills by reason of the physical qualities of such ground: its lightness and good drainage. Thus the Archer's Dart, *Agrotis vestigialis* Hufn., Caradrinidae, feeds upon several bed-straws, *Galium*, and a number of common grasses but, with some interesting exceptions, lives only on sandy coasts. However, it is quite common far inland in the Breck district of Suffolk and Norfolk (pages 33-4) which is extremely sandy, and it is to be found in a few other sandy places in the centre of England: Cumnor near Oxford, for instance, where a hill above the Thames is crowned by a cap of almost pure sand in which sand pits have been dug. Clearly the frequency of the species round our shores is determined by the nature of the ground there rather than by any need for a maritime environment.

As is to be anticipated among those moths which have succeeded in living here at the edge of their range by adjusting themselves to special types of environment, some have concentrated upon adaptations to coastal conditions. A good example is supplied by the Ground Lackey, *Malacosoma castrensis* L., Lasiocampidae, which is strictly confined to salt marshes in the south-east of England (Map 9), though the larva (Plate 23, figure 2) feeds upon almost any kind of plant growing in such places. In Continental Europe it occurs on heaths and in woods and has no special connection with the shore. Here it has probably had to fit itself to some specially chosen habitat in the manner indicated, while its geographical distribution in this country is probably related to the special need for sunshine which is a marked characteristic of its larvae. They sun themselves fully exposed whenever possible, and are then extremely conspicuous, being protected by their hairs, warning coloration, and by their gregarious habit when young. Moreover, they can only be reared in captivity if given plenty of air and sunshine. It is not surprising, therefore, that they should favour the semi-Continental climate of South-East England. The Essex Emerald, *Euchloris smaragdaria* Fab., Geometridae, provides an even more extreme instance of the same kind. In Britain the larva feeds only on Sea Wormwood, *Artemisia maritima*, and the moth is confined to the Essex salt marshes, though abroad it is not at all restricted to the seaboard.

Rocky coasts and cliffs in general supply good localities for coastal species, but not many of them are limited to this environment to the exclusion of the normal shore. A species which appears entirely to be so in its few haunts in the Isle of Man, the island of Canna and in Ireland is the Grey, *Hadena caesia* Schiff. (Plate 26, figure 4), Caradrinidae, though for what reason is unknown (page 119). It feeds upon Campions, *Silene maritima* and *S. inflata*, which are widespread around our shores. Similarly the Scarce Blackneck, *Ophiusa craccae* Schiff., Plusiidae, feeds as a larva upon Wood Vetch, *Vicia sylvatica*, but it occurs only on rocky coasts in Devon and Cornwall. The Black-banded, *Antitype xanthomista* Hb., Caradrinidae, is also restricted to sea cliffs within very much the same area except that it is also found in the Isle of Man (Map 5). It feeds on Thrift, *Armeria*, and plantain. On the other hand the Marbled Coronet, *Hadena conspersa* Schiff., Caradrinidae, though living in a series of differing sea-side conditions and even in a few places inland, certainly favours shingle beaches above all other haunts.

BRECKLAND

A parallel has already been drawn between the type of habitat provided by sandy shores and that found in the Breckland of Norfolk and Suffolk. This is a wide expanse of country in the neighbourhood of Tuddenham and Brandon quite unlike any other in Britain. Its fauna and flora are remarkable and unique, and until recent years they have been guarded by private owners. Now that the tendency of taxation is to drive the landlord to ruin or the auction sale, public authorities, with that disregard for the countryside which has so often characterised their activities in Britain, have descended upon this remarkable district to afforest it and to convert it into aerodromes and agricultural land: a fate which the Nature Conservancy (a chartered body under the Privy Council) has come too late to avert, for the areas which it may be possible to save will almost certainly be too small to maintain the general characteristics of the region. The photograph on Plate XXI will serve as a memento of it.

Breckland consists of a great exposure of wind-blown sand formed from the drying of the upper surface of a layer of boulder clay laid down in glacial times. Beneath the clay is chalk with beds of flint. Apart from the constant drifting of the sand owing to wind action, no marked geological changes have taken place here since the Neolithic Period. As already indicated, the flora and fauna it supports are of a highly exceptional kind, and a number of moths are found nowhere else in Britain.

Some of these unique species of the Breck are localised there on account of their food plants, which are peculiar to that area. Thus the Viper's Bugloss, *Anepia irregularis* Hufn., Caradrinidae (Map 7), a moth named after a herb with which it has no connection, feeds as a larva upon the Spanish Catchfly, *Silene otites*, which grows nowhere else. On the other hand, the food of some of the insects characteristic of this district is to be obtained widely outside it. Thus the Spotted Sulphur, *Emmelia trabealis* Scopoli (Plate 26, figure 10), Plusiidae, eats the Common Bindweed, *Convolvulus arvensis*, but the insect is absent elsewhere in Britain save for a few casual examples, mostly caught many years ago. The distribution of the Grey Carpet, *Lithostege griseata* Schiff., Hydriomenidae (Plate 26, figure 13), is equally restricted here, but its food plants, the Flixweed, *Sisymbrium sophia*, and the Treacle Mustard, *Erysimum cheiranthoides*, are widespread. On the Continent of Europe this is an insect of rather southern distribution and it has doubtless had to adjust itself closely to this special type of locality to maintain itself in this country.

Fens and Marshes

The moths of fens and marshes are an immense assemblage. Whole groups, such as the 'Wainscots' among the Caradrinidae (including such genera as *Nonagria*, *Coenobia*, *Chilodes*), are adapted to this type of environment while many species, widely scattered from a classificatory point of view, are well known to be strictly confined to such places and often have the colour-pattern which adapts them to rest among reeds; they may therefore differ superficially to a marked degree from those to which they are most nearly allied. Instances of this kind have been given in discussing protective devices (page 94), and examples of some of the special features of this community of reed moths were then mentioned. Furthermore, the habitats of other marsh plants are sometimes so circumscribed that the species which feed upon them are strictly limited by their distribution. Thus the larva of the Silver Barred, *Eustrotia olivana* Schiff., Plusiidae, found at Wicken and one other fen in Cambridgeshire, and locally in bogs in Kerry, eats the marsh grass *Molinia caerulea* (Map 3). The Dotted Fan-foot, *Zanclognatha cribrumalis* Hb., Plusiidae, feeds only upon marsh grasses of the genera *Carex* and *Luzula*. The food of the resplendent Scarce Burnished Brass, *Plusia chryson* Esp., is restricted to Hemp Agrimony, *Eupatorium*, a plant found on the whole in damp situations, so that this insect is principally to be obtained in fens. It is noteworthy, however, as always in considering species strictly confined to certain habitats, that many examples could be given of marsh moths whose food-plants grow in damp and dry situations alike: as the Marsh Pug, *Eupithecia pygmaeata* Hb., which eats Mouse-ear Chickweed and Stitchwort, *Stellaria holostea*; or the Oblique Striped, *Orthonama vittata* Bork. (Plate 17, figure 6), both Hydriomenidae, an insect especially associated with fens and water meadows whose larva feeds on common Bedstraws (*Galium saxatile* as well as *G. palustre*).

The drainage of most of the true fens of Cambridge, Huntingdon and East Anglia, and the constant encroachment upon marshes and bogs taking place to-day under pressure to obtain agricultural land, is seriously menacing a flora and fauna unique in this country. It is true that some of these areas are being preserved by private owners, the Nature Conservancy and other bodies, but this does not in all circumstances secure them. For in some places the pumping by which land is being reclaimed or maintained for agriculture in the neighbourhood, is so reducing the water table, that it will not be possible to preserve indefinitely the characteristics of the protected fens. This danger threatens Woodwalton in Huntingdonshire. It is less acute at the most famous of the fens, Wicken near Cambridge. Fortunately the peculiar features of the marsh community of the Norfolk Broads (Plate XXII) appear to be in less immediate danger. However, it is essential to maintain examples of several types of Fenland: Woodwalton, Wicken and the Broads each possess species of moths not found in the others, while in all of them a sufficiently extensive acreage must be preserved to supply a fair sample of the varied ecological conditions of the locality, for these each hold their appropriate Lepidoptera. Thus Caradrinidae such as the Dissolute Moth, or Brown-veined Wainscot *Nonagria dissoluta* Treit., and the Reed Wainscot, *N. algae* Esp., are to be found in actual reed-swamp, where the Flame Wainscot, *Senta flammea* Curtis, and Fenn's Wainscot, *Arenostola brevilinea* Fenn. (Plate 26, figure 8), would often be searched for in vain even within the district which they inhabit, for these are insects of mixed reed litter and generalised marsh plants. The rare and remarkable Marsh Moth, *Hydrillula palustris* Hb. (Plate 17, figures 1 and 3), lives where swamp and drier land meet. This strange insect is one which long remained, and indeed to some extent still is, a great rarity owing to our ignorance of its habits. The males come to light, but rarely and capriciously. It is known that the small-winged heavy-bodied females (figure 3) can fly, though as far as we are aware they hardly ever do so and almost all the imagines that are caught are males. However, the larva has now been found and successfully bred, and the food in nature, Meadow-sweet, *Spiraea ulmaria*, has been ascertained. The insect is an inhabitant of Fenland, though a single worn specimen was found on the Lincolnshire coast, but one extraordinary colony seems also to exist in the neighbourhood of Carlisle in Cumberland; if, indeed, the few specimens casually captured there are really the same species. It is suspicious that out of less than ten specimens known to have been taken, the first two were females found flying, an almost unprecedented occurrence in *H. palustris*.

Though the true Fen district, together with the Broads, contains by far the greatest assemblage of marshland moths, a considerable number of the species are of wide distribution and some of them found elsewhere are absent from that favoured area: for instance,

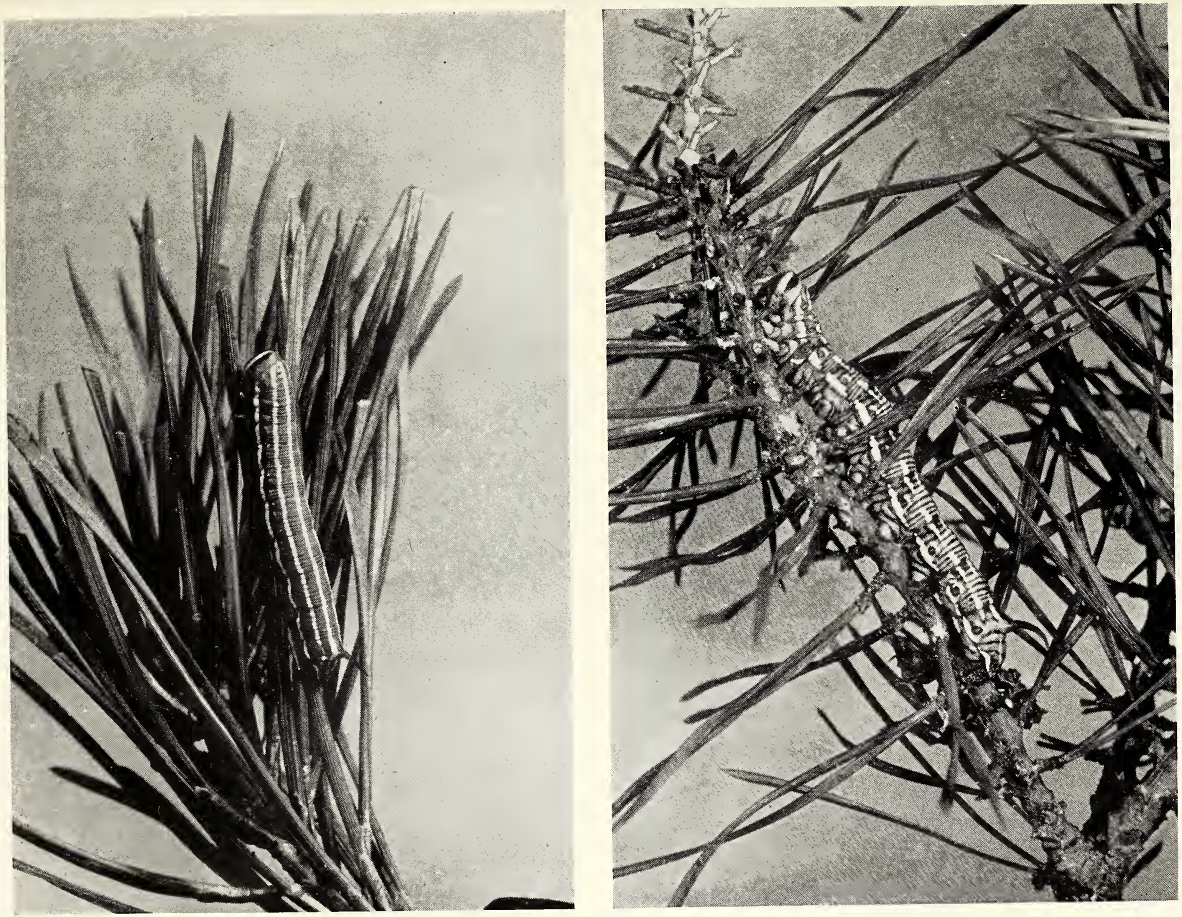
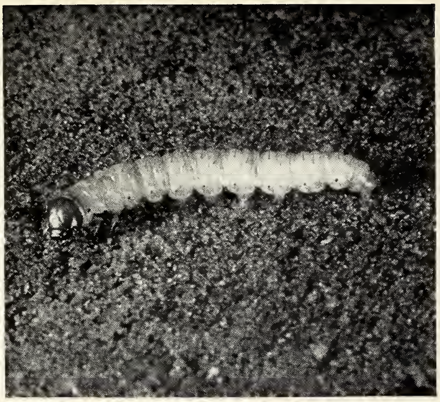


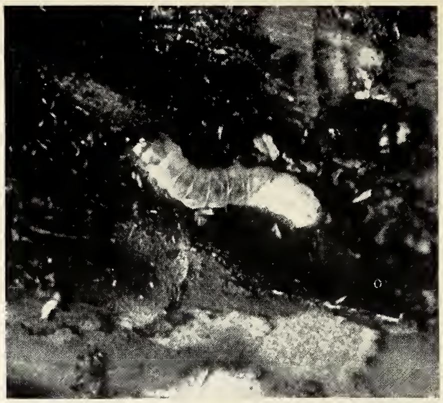
Plate XV. LARVAE OF PINE HAWK (*Hyloicus pinastri*)

1 Fully grown (X 1)

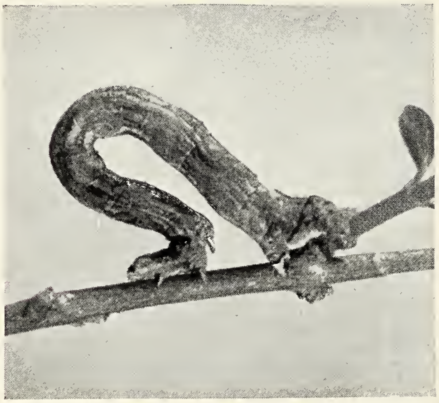
2 Partly grown (X 1. 5)



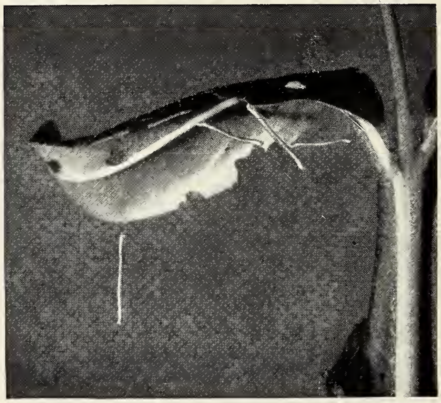
1. Common Swift, *Hepialus lupulinus* (X 1.25)



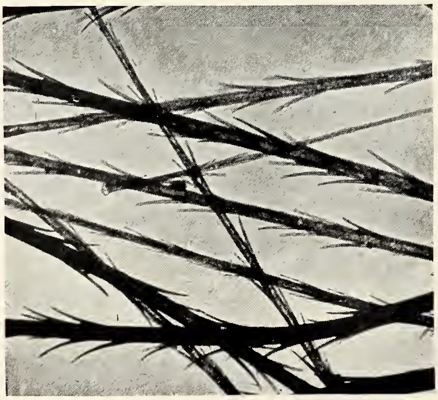
2. Red-belted Clearwing, *Aegeria culiciformis* (X 1.25)



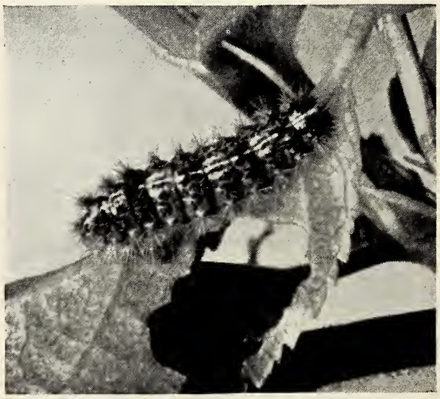
3. Waved Umber, *Hemerophila abruptaria*, fully grown (X 2)



4. Waved Umber, *Hemerophila abruptaria*, young (X 2)



5. Hairs of the Gold-tail larva, *Euproctis chrysorrhoea* (X 80)



6. Short-cloaked Moth, *Nola cucullatella* (X 4)

Plate XVI. LARVAE

Webb's Wainscot, *Nonagria sparganii* Esp., Caradrinidae, which is established along the south coast of England and in Co. Cork, Ireland.

There is one moth which, though occurring rather uncommonly in the 'Fens,' is really characteristic of a very different terrain; that is to say, moorland bogs. This is Haworth's Minor, *Celaena haworthii* Curtis, Caradrinidae, a species localised by its sole food-plant the Cotton-grass, *Eriophorum vaginatum.*

Few species of moths are especially denizens of river banks, but two such insects may be mentioned here. One is the Butterbur, *Hydraecia petasitis* Dbl., Caradrinidae, the larva of which feeds in the roots of the plant after which it is named, *Petasites.* It was formerly thought to be confined to Southern Scotland and the North of England, but it is a retiring insect difficult to find and is now known to occur widely in Britain. The other, the Scarlet Tiger, *Panaxia dominula* L., Hypsidae, (Plate 15) is of southern distribution, being found from Kent to Devon principally south of the Thames, though specimens have been taken as far as North Staffordshire (Map 10). It feeds on the Comfrey, *Symphytum officinale,* growing on the banks of rivers and undoubtedly this is its favourite haunt, though it may spread up into and colonise marshes. The fact that this species has been able to adapt itself to two wholly exceptional types of habitat, the Pendine Sands in Wales and a locality at the foot of chalk cliffs on the coast of Kent, does not affect the truth of this generalisation, though it does illustrate that a moth may sometimes adjust itself to abnormal conditions, as so often in the isolated English populations of species widespread in Continental Europe.

Heaths and Moors

The moths of heaths and moorland are a heterogeneous assemblage whose characteristic, but not universal, feature is some adaptation to living upon heathers, *Erica* species and *Calluna.* Most of the insects which expose themselves by day upon these plants, whether feeding on them as larvae or resting upon them as imagines, have a distinctive colour-pattern which renders them inconspicuous. The fore-wings of the Beautiful Yellow Underwing, *Anarta myrtilli* Caradrinidae, L. (Plate 16), illustrate it excellently. The hind-wings are yellow with a broad black border. They are always concealed when the insect is at rest but provide a flash colour (page 97) when it flies. The same type of cryptic colouring is adopted by many other species found upon moors; for instance, the True Lover's Knot, *Lycophotia porphyrea* Schiff., and the Heath Rustic, *Amathes agathina* Dup., both Caradrinidae, and the Narrow-winged Pug, *Eupithecia nanata* Hb., Hydriomenidae. The netted pattern of the Common Heath, *Ematurga atomaria* L. (Plate 9, figures 1 and 2; Plate 16), Selidosemidae, is also well suited to an insect which lives among heather. On the other hand, the imago of the Grey Scalloped Bar, *Dyscia fagaria* Thnbg., Selidosemidae, rests with wings outspread upon the dark peaty earth and is so coloured that it is often mistaken for a whitish stone and passed by unnoticed. The Neglected, *Amathes castanea* Esp., Caradrinidae, which is as much an insect of heather as any of those just mentioned is, however, of a uniform grey colour, nor would the larva be hidden were it to feed exposed during the day. This, however, it does not do; for it conceals itself among low herbage until dusk, when it becomes active. Similarly the moth rests out of sight among roots and low herbage until the late evening.

There are, of course, many moorland species that feed upon plants other than heather or ling, such as the two moths of the Eyebright, *Euphrasia*. These are the Heath Rivulet, *Perizoma minorata ericetata* Curtis, and the closely allied Pretty Pinion, *P. blandiata* Schiff., Hydriomenidae, both of them northern insects in Britain. A further example of a strictly moorland moth unassociated with heather or ling, is the Manchester Treble-bar, *Carsia sororiata* Hb., Hydriomenidae. It feeds as a larva upon Cowberry, *Vaccinium vitis-idaea* and Cranberry, *V. oxycoccos*.

The larvae of a certain number of heathland moths are capable of feeding both upon heathers and many other plants, and accordingly some of the species are not strictly confined to that type of terrain. The Emperor Moth, *Saturnia pavonia L.* (Plate 18), though pre-eminently an insect of the moors, feeds principally but not exclusively upon *Erica* and *Calluna*. Its larval and pupal adaptations have been discussed in Chapter 7. The imago seems to be warningly coloured and upon this the female apparently depends for protection, for she sits sometimes exposed during the day and becomes active only in the evening. The males, however, scour wildly over the moorlands in late April or early May. Their powerful flight and the rough ground they frequent makes them difficult to capture. The habits of the large Northern Eggar, *Lasiocampa quercus callunae* Palmer, are very similar, except that the moth flies in late May and June. It, too, feeds upon a wide variety of plants including heather, and while principally an insect of the moors of the north it strays to some extent beyond the confines of such places. The larva makes no effort to hide itself, being protected by a thick coating of irritant hairs. This is a northern form of the Oak Eggar, *L. q. quercus* L., which frequents lanes, heathy commons, sandy shores and cliffs in the South of England. It flies in July and August, for its life-cycle is completed in twelve months, and the larva, hibernating when very small, requires most of the summer in which to feed. The northern race *callunae*, on the other hand, lives two years, about twenty months of which are passed as a larva. Indeed, it is a characteristic feature of the insects of the far north that, limited by the short summer and almost non-existent spring and autumn, they require two or more seasons in which to feed and accumulate sufficient reserves for metamorphosis. This is a tendency which may perhaps be extended to a lower latitude in large insects. The Northern Eggar is a moth of considerable size, a female often measuring 3½ inches across the expanded wings, so it may well be that in the North of Scotland and in the Orkneys a single summer does not allow time for it to complete its growth. It does not seem likely, however, that this is still a limiting factor farther south, and the range of the *callunae* form extends to Northern England. Possibly this race originated in a northern climate and has for some reason spread southwards.

Many of the heaths of Southern England are but isolated relics of far more extensive tracts of moorland country. Thus the moths, like the rest of the fauna and flora inhabiting them, have often become sub-divided into small isolated communities. The opportunities for special evolutionary adjustment which such ecological conditions can provide will be discussed on p. 222.

Chalk Downs

Chalk soils are alkaline, and arid because porous, and they provide a complete contrast to heather moors, which are acid and moist. These differences have a great influence on their ecology; also the background-colour of peaty soil is dark brown or blackish and of the chalk light grey or white. Moreover, though heaths are to be found in all parts of Britain they are especially characteristic of the North and West, but the chalk is restricted to the South and East, not ex-

Plate 17. MARSH MOTHS AND RELATED SPECIES

1
Male
WOOD-WALTON
HUNTINGDONSHIRE

2
WARRINGTON
LANCASHIRE

3
Female
WOOD-WALTON
HUNTINGDONSHIRE

4
THURSBY
CUMBERLAND

5
COTHILL
BERKSHIRE

6
NEW FOREST

7
TUDDENHAM
SUFFOLK

8
YARMOUTH

9
CAMBRIDGE

10
WICKEN

11
fully grown larva
ESHER

12
fully grown larva
WICKEN

13
WICKEN

14
THURSBY
CUMBERLAND

15
fully grown larva
WICKEN

16
fully grown larva
LONDON

---

1 and 3. Marsh Moth, *Hydrillula palustris;* 2. Fen Wainscot, *Arenostola phragmitidis;* 4. Small Wainscot, *Arenostola pygmina;* 5. Small Rufous, *Coenobia rufa;* 6. Oblique Carpet, *Orthonama vittata;* 7. Silky Wainscot, *Chilodes maritima;* 8. Shore Wainscot, *Leucania litoralis;* 9 and 11. Southern Wainscot, *Leucania straminea;* 10 and 12. Powdered Wainscot, *Simyra albovenosa;* 13 and 15. Dark Dagger, *Apatele tridens;* 14 and 16. Grey Dagger, *Apatele psi*

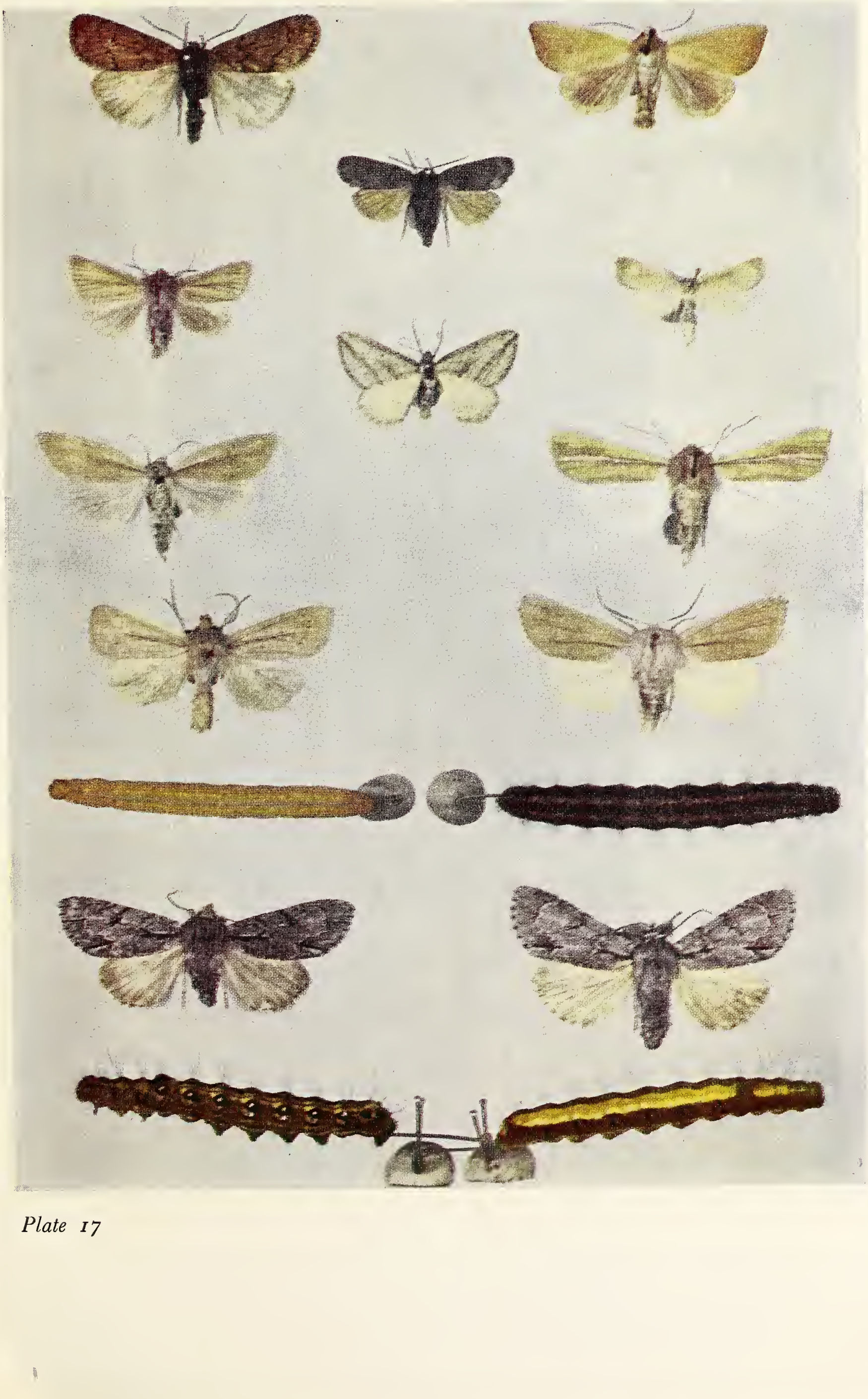
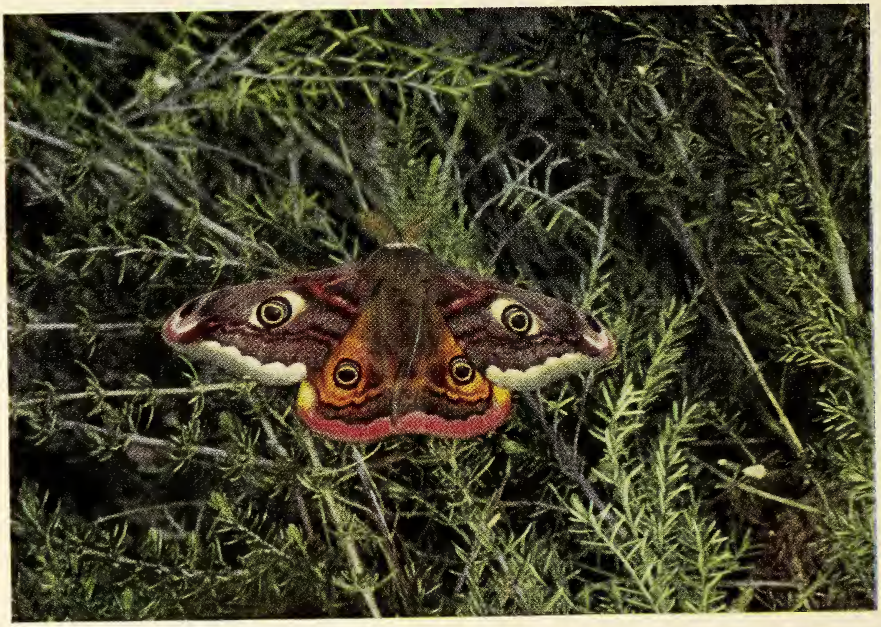


Plate 17



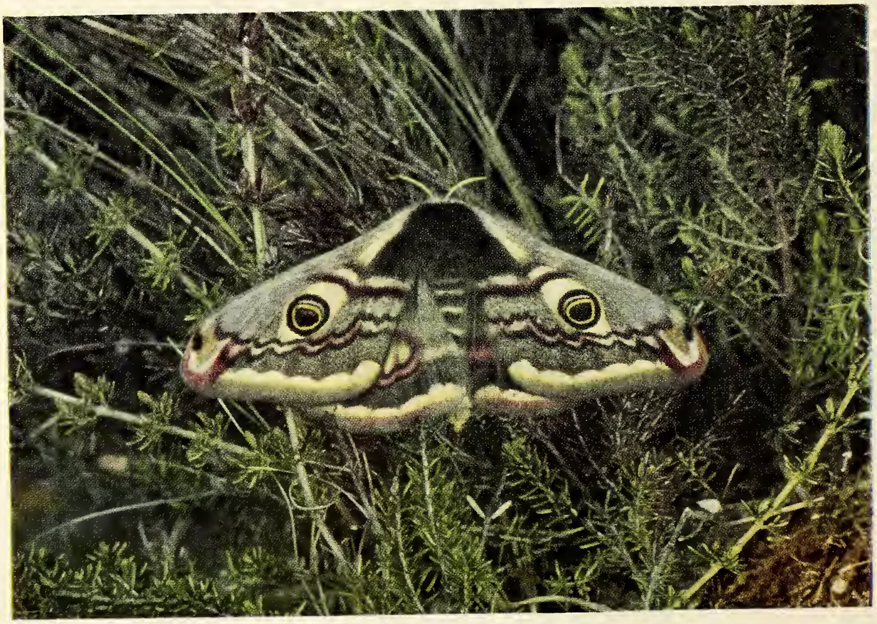


Plate 18. Emperor Moth, *Saturnia pavonia*

1. (*above*) Male
2. (*below*) Female

tending beyond a line running diagonally from Dorset to Flamborough Head inYorkshire. However, limestones are far more widely distributed, and the principal features of the chalk are reproduced on them also, though in a less marked degree.

It is not possible in a short space to give an account of the moths which inhabit chalk downs and limestone hills. Some of the species are restricted to these localities entirely by their food-plant. Thus in Southern England the juniper is pre-eminently a tree of the chalk downs, one to which the Juniper Carpet, *Thera juniperata* L., Hydriomenidae (Plate 28, figure 10), is wholly confined. However, it is also abundant among juniper trees wherever these grow in Scotland, in the North-west of England and in a few places in North Wales. But a different race of the moth is associated with this northern region (figure 11), this is smaller and more strongly marked than that of the chalk downs of South-east England. The Pretty Chalk Carpet, *Melanthia procellata* Schiff., Hydriomenidae, is to be found in many parts of Southern England but only where the soil is alkaline, being restricted to such districts by the distribution of its sole food-plant, the Traveller's Joy, *Clematis vitalba*. So too are a few other species, such as Haworth's Pug, *Eupithecia isogrammaria* H.-S., and the Small Waved Umber, *Horisme vitalbata* Schiff., both Hydriomenidae (Plate 20, figure 4). Also the Cistus Forester, *Procris geryon* Hb., Zygaenidae, a small bronze-green species very similar to the female Scarce Forester (Plate 26, figure 12). Its larva feeds on Rock Rose, *Helianthemum*, but only where that plant grows on chalk or strongly alkaline soil. The moth is day-flying, and makes a delightful picture as it sits on the yellow flowers of its food-plant. A locality for this and other chalk species, such as one of the races of the Five-spot Burnet, *Zygaena trifolii* Esp., and the Juniper Carpet, is shown in Plate XIX.

The Black-veined Moth, *Siona lineata* Scopoli, Selidosemidae, seems to feed upon *Brachypodium pinnatum* in nature. This being strictly a grass of chalk and limestone areas limits it to such places, but there must be additional factors of whose nature we are ignorant which restrict it almost entirely to the chalk downs near Wye in Kent: a former locality for it in Sussex has unfortunately been destroyed. Indeed, as so often with moths having marked habitat-preferences, the reasons why some species are strictly confined to chalk and limestone are quite unknown and are at any rate not directly connected with their food-plants. Thus the Chalk Carpet, *Ortholitha bipunctaria* Schiff., Hydriomenidae, a most typical insect of chalk and limestone hills (Map 8), feeds upon clovers and trefoils, while the Feathered Ear, *Pachetra sagittigera* Hufn., Caradrinidae, which has a restricted distribution on the chalk (page 119), eats such ordinary grasses as *Poa annua.* It seems likely, however, that the cell-sap of such plants tends to be more alkaline when growing upon chalk or limestone soil, and this may well constitute a limiting factor in the distribution of certain moths. Naturally all those associated with the plants characteristic of acid soils, such as heathers and the foxglove, will be absent from the alkaline regions of Britain, so that the Lepidoptera reflect to some extent the characteristics of the soil.

Woodlands

There is no need to discuss the moths of woodlands in any detail, for their food-plants are often a sufficient explanation of their habitats. Thus those which are restricted to beech woods form a sharply marked ecological association, frequently characterised as imagines by a colouring which harmonises with that of withered beech leaves and gives a close superficial similarity to species which are but distantly related: for instance, the Barred Hook-tip, *Drepana cultraria* F., Drepanidae, and the Clay Triple-Lines, *Cosymbia trilinearia* Bork., Sterrhidae. Some other moths confined to beech woods are, however, not of this distinct hue. A rather curious example is provided by Blomer's Rivulet, *Discoloxia blomeri* Curtis, Hydriomenidae, which, though feeding on Wych-elm, *Ulmus montana*, seems never to be found away from beech trees, upon the trunks of which it habitually rests. It is a whitish insect marked with black and a small orange patch.

Oak and mixed deciduous woods have also their characteristic species. Those of ash and yew are, of course, specialised and fewer in number, for woods composed of these trees are relatively uncommon. Though the various poplars and the great assortment of British willows do not form forests in this country, groves of them are to be found in damp places, while they often fringe river banks. A distinctive assemblage of moths feeds upon them, and those which bore into the wood or live in the shoots and below the bark sometimes do considerable damage to these trees (page 115). Mention must also be made of the Lepidoptera of birch scrub which, especially in the north, supports a large number of moths. The magnificent Large Emerald, *Geometra papilionaria* L., is one of the most characteristic insects of such places. It is a brilliant green and sometimes more than two inches across the expanded wings. The Grey Birch, *Ectropis punctulata* Schiff., Selidosemidae, is found in similar situations, and its grey ground-colour and small black markings conceal it effectively as it sits with wings outspread upon a birch trunk. Several of the early spring moths feed upon this tree and fly round it or rest upon it at the season when the leaf buds are bursting. The Yellow Horned, *Achlya flavicornis* L. (Plate 25), Polyplocidae, may be seen sitting upon the twigs or the stems of the smaller bushes in March and April, while on sunny days at approximately the same season the males of the Orange Underwing, *Brephos parthenias* L. (Plate VII), Brephidae, fly round the upper branches of the taller trees, looking black against the sky; the females are more lethargic but readily take to the wing when disturbed. Another moth of extremely different appearance and affinities, but with similar habits, is the Kentish Glory, *Endromis versicolora* L. The males fly in the sunshine and 'assemble' (pages 10-12) strongly to the females, which become active only in the late evening. It is a large and beautiful species with a discontinuous distribution, being known as a rarity in a number of the forests of Southern but not Northern England, yet occuring much more frequently, in Scotland.

Special Habitats

Certain special areas or localities, some large others small, deserve brief consideration here on account of the exceptional species which they support. A few moths are curiously limited to the centre of England, having a distribution somewhat reminiscent of the Chequered Skipper, apart from its Scotch race (*Butterflies*, page 135). The Angle-striped Sallow, *Enargia paleacea* Esp., Caradrinidae, is a good example of them. It feeds upon birch yet, except for rather casual occurrences, it is in England restricted to the Sherwood Forest area of Nottinghamshire and to South Yorkshire, though it also occurs in the Scottish Highlands. The factors which thus curtail its distribution are unknown. Similarly the Union Rustic, *Apamea pabulatricula* Brah., also a member of the Caradrinidae, is almost confined to woods in Lincolnshire and Nottinghamshire (Map 4).

The New Forest area is a habitat extraordinarily favoured by Lepidoptera, but the attributes which make it so have never been analysed. It is, of course, an extensive and largely unspoilt region containing a wide variety of habitats of woodland (*Butterflies*, Plate xx) and heath, one moreover that is situated close to the south coast where it obtains a favoured climate, and doubtless these considerations are important. Its peculiarities have to some extent been indicated in the previous volume of this work, in which it was pointed out that this is the only place in Britain where the females of the Silver-washed Fritillary are dimorphic. The insect is widespread throughout the South of England and in Ireland, but the *valesina* form, a dominant, sex-controlled to the female, occurs only as a rare aberration elsewhere.

This is to the entomologist an almost fabulous region, for many species can be obtained nowhere else, while others common enough here are great rarities elsewhere. It is possible only to indicate a few of them. The two resplendent Crimson Underwings, *Catocala sponsa* L., and *C. promissa* Schiff., Plusiidae, like smaller and more intensely coloured forms of the Red Underwing (Plate 5) are common only there and in some Kentish woods. Our two species of Cochlididae, the Festoon, *Cochlidion avellana* L. (Plate 2 larva, Plate 16 imago) and the Triangle, *Heterogenea asella* Schiff., are much more frequent in the woods of this area than in any other part of Britain. Two extinct moths, the New Forest Burnet, *Zygaena meliloti* Esp. (Plate 26, figure 14) and the Speckled Beauty, *Cleora arenaria* Hufn. (Plate 32, figure 5), Selidosemidae, probably owe their destruction to their extreme localisation to this district, but their disappearance will be discussed in Chapter 14. It may be added that a considerable number of uncommon species are more frequent in the New Forest than elsewhere: for instance, the Dingy Mocha, *Cosymbia orbicularia* Hb., Sterrhidae, the Marbled Pug, *Eupithecia irriguata* Hb., Hydriomenidae, and the Dotted Carpet, *Cleora glabraria* Schiff., Selidosemidae.

Among the numerous seaside localities which support an unusual fauna of moths two may be selected for brief comment here. The first of these is Folkestone Warren (Plate xxi), which is in many ways a remarkable place. Geologically it is the result of a slip-fault, where chalk rests upon the greasy surface of gault which dips towards the sea. This produces a land-slide area between the chalk cliffs and the shore in which piles of fallen debris, with swamps here and there among the rough ground, provide the ecological requirements needed for many rare plants, also for a singular assortment of Lepidoptera some of which exist nowhere else in Britain even though their food plants may be of widespread occurrence. For instance, this and Herne Bay seem to be the only habitats of the Fiery Clearwing, *Aegeria chrysidiformis* Esp., Sesiidae, though the larva feeds on the roots of sorrel and dock, *Rumex*. In these two places it appears to be an established native. It is almost true to say that the Sub-angled Wave, *Scopula nigropunctata* Hufn., Sterrhidae, has never been taken in Britain but in the Warren and its immediate neighbourhood. It was discovered there in 1859 and continued to be captured regularly until about 1890. Since that date only occasional specimens were seen up to 1912, when it apparently became extinct. However, one came to light a mile from the Warren in 1946. This may either mean that the original colony has lingered on in numbers so small as to escape attention or that the locality has been colonised by a new immigration from the Continent. The latter alternative is the more likely, for Folkestone is on one of the recognised migration routes, and the moth next to be considered has almost certainly re-populated the locality from France. There are indeed many species which, arriving as immigrants in Britain, can maintain themselves for a number of years until destroyed by an unusually severe winter, by parasites adapting themselves to prey upon them, or by an extreme reduction in numbers which only a large colony can withstand (pages 79-85). The French race of the Swallow-tail Butterfly, *Papilo machaon* L., as opposed to our British sub-species which is a resident in the Fens, is just such a settler which, arriving in Kent at intervals, may survive there for a year or two (*Butterflies*, pages 302-304). Evidently the Sub-angled Wave had a better hold upon the locality than this, for it seemed already well established in its extremely restricted haunt when discovered, and it survived there for forty years or so.

The species just mentioned as almost certainly a transient colonist at Folkestone Warren is the Rest Harrow, *Aplasta ononaria* Fuessly (Plate 3, figure 5) Brephidae. This has never been found in any other British locality except at Sandwich. It was first reported in the Warren in 1866 and some further specimens were taken during the next few seasons, when it apparently became extinct. However, in 1937, after a lapse of over sixty years, it reappeared again not uncommonly, and the colony has ever since maintained itself at Folkestone. Yet I should be surprised if it continued to do so indefinitely, though the larger population at Sandwich may possibly survive. It is likely that one of the causes just indicated will destroy it. Though the moth feeds upon the widely distributed plant after which it is named, *Ononis*, the strange conditions of the Warren and of the Sandwich area supply the only situations in which it can make even a temporary home in this country, for it is a species of central and southern Europe.

The second exceptional seaside locality to which attention will be drawn is provided by the sandhills in the neighbourhood of Deal in East Kent. Here are to be found several moths otherwise of great rarity in Britain. This is the headquarters of the Pigmy Footman, *Eilema pygmaeola* Dbl., Arctiidae (Plate 26, figure 15), already mentioned as almost peculiar to this country. It occurs also, though apparently in much smaller numbers, elsewhere on the coasts of Kent and of Norfolk. Similarly, though the Bright Wave, *Sterrha ochrata* Scopoli, has in the past been found on the coast of Essex and at a few other places, it is pre-eminently a Deal insect. It feeds upon a number of common plants (Dandelion, Coltsfoot and others). If the British race be distinct from that on the Continent as claimed by Prout, who named it *Ssp. cantiata*, this must be an ancient member of our fauna, unlike the two colonists of Folkestone Warren to which reference has just been made. However, as suggested by Mr. R. F. Bretherton (1951), rightly I believe, Deal has also supported for a time one of these temporary visitors. This is the Scarce Black Arches, *Roeselia aerugula* Hb., Nolidae. It was first found in the Isle of Wight in 1858 where it continued to be caught for some years. Subsequently it was taken on several times at Folkestone, presumably in the Warren, and near Dover; however, it was far more frequent at Deal than elsewhere, whence it vanished about 1903. It is said that it was over-collected and that its extremely limited habitat was finally destroyed by the making of golf greens. Yet Bretherton points out that these causes did not operate in its other localities and that its history in this country is strongly suggestive of the situation in which the progeny of scattered immigrants survive for some generations but are unable to establish themselves permanently. On the other hand, the species is apparently not recorded from the Channel coast of France or Belgium, but it is so small and unobtrusive that no great weight can be attached to that circumstance.

One curious locality which deserves at least passing mention is that provided by the parks and tree-lined streets of London. Though no species is confined to these places, it is certainly true that some moths appear to be markedly commoner there than elsewhere. I would mention among them several members of the genus *Apatele*, Caradrinidae, in particular the Sycamore, *A. aceris* L., and the Poplar Grey, *A. megacephala* Schiff.: also the Waved Umber, *Hemerophila abruptaria* Thnb. (Plate 20) and the Brindled Beauty, *Lycia hirtaria* Clerck (Plate XIII, figures 8 and 9), both Selidosemidae. Nor is this very surprising. The effects of human interference on the countryside are generally disadvantageous both to animal and plant life, but here and there the ecology is so altered as even to benefit certain species, perhaps through the destruction of their predators or because their physiology chances to accord with the changed conditions. Indeed, the latter circumstance is partly responsible for the spread of dark varieties of Lepidoptera in industrial areas, including in some instances, London itself (Chapter 13).

It has already been pointed out that a selection only of the more celebrated localities, chosen to illustrate various ecological conditions, can be described here. In addition, others colonised by migrant species or supporting a relict fauna are considered respectively in Chapters 6 and 11.

Finally one other habitat, the remarkable characteristics of which have only recently been discovered, must briefly be mentioned: that is to say, the area of oak and aspen woods in the neighbourhood of Ham Street in Southern Kent. It is now certain that a number of moths breed there, possibly as established residents, which until a few years ago were known only as great rarities, while several of them were regarded merely as casual immigrants to this country.

The most spectacular of these is the great Clifden Nonpareil, *Catocala fraxini* L., Plusiidae, one of the largest of our moths, which may measure up to four inches across the expanded wings. It resembles a giant Red Underwing, but the hind-wings are black, crossed with a broad lilac coloured band. The larva feeds on aspen and large numbers of the imagines have now been taken at Ham Street both at light and at sugar and at rest upon the trees. This moth was also caught in Norfolk for several years in succession and seemed to be resident there, but that colony has apparently died out. The Clifden Nonpareil has recently become abundant in Denmark. It is probable, therefore, that it has extended its range northwards during a period when its numbers have greatly increased and has for the time being been able to maintain itself in England in colonies that may prove only temporary.

Perhaps more remarkable is the recent discovery that the Lunar Double-stripe, *Phoberia lunaris* Schiff., is well established not only in the Ham Street woods, but in one or two other localities in Kent and in mid-Sussex. This is also a member of the Plusiidae and was an even rarer insect, for there were only eleven fully authenticated records of it prior to 1940. It feeds upon oak, and the larva has now been found, especially upon the short stems growing from the stumps of trees recently felled. The imagines, which are on the wing in late May and early June, have been disturbed from leaves during the day and have visited sugar, but they are usually taken flying among oak stumps at night, when they must be pursued with lamps.

Other species of great rarity are apparently established and breed in this locality. One of them, the Cudweed Shark, *Cucullia gnaphalii* Hb., Caradrinidae, is an extremely scarce and local species which feeds as a larva upon Golden-rod, *Solidago.* It breeds also in a few other localities in Kent, Surrey and Sussex. Even less well known is the Lesser Belle, *Colobochyla salicalis* Schiff., Plusiidae. This is an aspen feeder which occurs in the Ham Street area. It has on a few occasions been taken elsewhere in Kent, in Surrey and in Sussex.

In 1950 a specimen of the Scarce Dagger, *Apatele auricoma* Schiff., Caradrinidae, was found newly emerged upon a tree in the Ham Street woods. This moth, always rare and restricted to Kent and Sussex, has long been apparently extinct. This is the first evidence for fifty years that it bred in Britain. One or two imagines have been taken on the Kent coast during this century. They were thought to be immigrants at the time, but it now seems possible that they originated from this locality.

It is likely that certain species can adjust themselves to the woods in the Ham Street area, and to some other places in South-east England, because they provide a habitat not unlike that to be found in Continental Europe. Some of the insects occurring there are probably but temporary colonists, the progeny of immigrants in recent years, though others may have arrived long ago but since the last Ice Age (Chapter 11). These may have been overlooked because they have unusual or secretive habits.

The localities discussed in this chapter are examples of many which deserve the attention of ecologists. When they have been studied by detailed ecological methods, the peculiar qualities which fit them to be the home of an exceptional moth fauna may possibly be discovered. An introduction to the techniques necessary for such work, and I may add to the point of view from which it should be conducted, is provided by Dowdeswell (1952), whose book *Animal Ecology* should be in the hands of all moth-collectors whose interest extends beyond their cabinets to the natural history of the species which they hunt.

CHAPTER II

RELICT FAUNAS

The Last Ice Age

A relict fauna is a survival from former conditions which have passed away. In one sense, therefore, it might be said that a large number of our species come within that definition, since the moths of many woodlands, downs and marshes persist as small isolated communities, remnants of the time when the countryside was in a primeval state and such habitats were of great extent. Here, however, we shall restrict the term to two types of survival in connection with the Pleistocene Ice Ages. First, as the ice retreated, those cold-loving forms which had flourished in the tundra and sub-arctic conditions in its neighbourhood followed it northwards to establish themselves in Northern Britain or to be marooned here and there on the tops of mountains where the climate approached that to which they had been accustomed. Secondly, some survivors from the warmth of the inter-glacial phases were able to maintain themselves during glacial periods. They did so in a few favoured places, both on the present land-masses and on low-lying country now submerged, for during the glaciations the sea was as much as 300 feet below its present level. These, as suggested by Beirne (1952), were (i) the land to the west and south-west of Britain, which included not only the Dumnonian Peninsula (Devon and Cornwall) and South, and especially South-west, Ireland, but also the area connecting these regions with one another and with the north coasts of France and Spain. Dartmoor to-day derives its unusual ecological qualities from the fact that it is the only ' mountainous ' region of Britain which has never been glaciated: (ii) The plain extending outwards from Wales under what is now the Irish Sea: (iii) The region which remained free of ice in the south of Britain, including part of the area now covered by the English Channel:

(iv) A tract of country in the south of what has become the North Sea, with the Dogger Bank, extending also into East Anglia and Cambridgeshire. To these I should add the relatively warm Atlantic area off the west coast of Scotland, including the present Western Isles and therefore the northern end of the land-connection with Ireland. These facts will briefly be discussed in the present chapter with the help of appropriate examples.

We live in a post-glacial era, probably an interglacial one, which was immediately preceded by the period of the most recent Ice Ages; that is to say, the Pleistocene. This included four glaciations, between each of which were long interglacial epochs, but we are here concerned only with the fourth or last glacial period during which the ice advanced and retreated three times, producing subsidiary glacial and interglacial phases.

The first glacial phase (of the fourth glaciation) was severe. At its maximum, most of the British Isles, except England south of the Thames and the south-west of Ireland, were ice-bound. It was followed by an interglacial phase warmer than to-day, during which, of course, the ice disappeared completely.

During the second glacial phase the ice did not extend so far as in the first, and it seems that England south of Yorkshire and the southern part of Ireland remained ice-free. In the following or second interglacial phase, though the climate was probably not quite so warm as to-day, the ice again disappeared.

The third or last glacial phase of the fourth glaciation was the least extreme. Only local glaciers existed on the higher ground and mountains of Scotland, North-west England, Wales and Ireland. The retreat of the ice initiated the Holocene period which continues to-day. This began somewhere about 9,000 B.C.; the land-connection with the Continent across the Straits of Dover was finally severed between 7,000 and 5,000 B.C. and with Ireland somewhat earlier.

From these considerations it will be realised that, as pointed out by Beirne (1952), glacial relicts may be the descendants of populations which invaded these islands during one or more of the three cold phases of the last main glaciation. Similarly, elements of a temperate fauna comprising interglacial relicts may have survived from either of the two interglacial phases, or even from the major interglacial period between the third and fourth Ice Ages of the Pleistocene. It will not generally be possible to distinguish between these various contributions to the two relict types in the following account, as the evidence for doing so is frequently inadequate.

Arctic-alpine Moths

We have in Britain a few truly sub-arctic species, survivors from the glacial phases. The most characteristic of these is a race of the Northern Arches, *Apamea exulis* Lefb. (Plate 30, figure 1), Caradrinidae, an Icelandic and Arctic moth which maintains itself in the Shetlands and is usually regarded as occurring nowhere else in Britain. Its distribution is limited by climatic factors, for it feeds mainly upon grasses. Like so many of these northern Lepidoptera, it requires two years, and sometimes more, to complete its growth (p. 139). As this insect followed the retreating ice northwards, it seems to have left behind it a race which managed to adjust itself to the conditions provided by mountainous areas on the Scottish mainland, in Perth, Aberdeen, Inverness, and even as far south as Arran. This is the dark form *assimilis* Dbl. (Plate 30, figure 2), which may have evolved into a distinct species. However, it is well to bear in mind that the species-concept is a genetic one. The taxonomist who determines specific status from anatomy is merely predicting what he believes would occur were an attempt made to breed the forms in question. When these closely approach one another, actual experiment and a study of the heterogametic sex among the offspring, if produced, is the only test; it is one which must be applied to this insect before the status of *A. exulis* and *A. assimilis* can definitely be determined. In this connection, it is worth noting that one or two specimens having the appearance of true Shetland *exulis*, with a yellowish ground-colour, have been taken among the *assimilis* population on the mainland. Either *exulis* exists as a separate species at a very low density there, or else its colour-pattern segregates as a rare variety in *assimilis.*

In these islands are to be found three species of the typical Arctic genus *Anarta.* This is circumpolar in distribution, and comprises a group of small day-flying Caradrinidae with cryptically marked fore-wings and flash-coloration on the hind-wings. This makes them extremely difficult to follow as they dart at great speed over mountain or moorland in bright sunshine. The Small Dark Yellow Underwing, *A. cordigera* Thnbg. (Plate 27, figure 15), is restricted to Scottish mountains, chiefly in Perth, Aberdeen and Inverness, but occurs down to elevations of less than 1,000 feet. Its distribution is controlled by the presence of the Bearberry, *Arctostaphylos*, upon which the larvae feed, while the imagines visit its flowers. Indeed, they are most easily caught when doing so, but their flight is so rapid and they are so difficult to see that it is most rewarding to creep up and suddenly to bring the net down upon a plant when, at the right place and season, which is the latter part of May, a specimen may fly up into the bag if this be kept raised. The Broad-bordered White Underwing, *A. melanopa* Thnbg. (Plate 27, figure 16), has a wider range, extending northwards from Perth and including the Shetlands (Map 1). It feeds on Crowberry, *Empetrum*, and apparently on Bilberry, *Vaccinium myrtillus*, but is restricted to greater heights and ascends to three thousand feet. Our third member of the genus, the Beautiful Yellow Underwing, *A. myrtilli* L. (Plate 16), is found on moors throughout the British Isles, where the larva feeds upon heather and ling (*Erica* and *Calluna*). This is a strange distribution for a member of this genus, but just as a race of *A. exulis* was able to establish itself in Central Scotland as it followed in the wake of the retreating ice, so this potentially northern species has been able to achieve a wide toleration of climate. Any physiological adjustments which were required in the process have not been reflected in changes of its colour-pattern.

The Netted Mountain Moth, *Isturgia carbonaria* Cl. (Plate 27, figures 13 and 14), Selidosemidae, is found in restricted localities at considerable altitudes on mountains throughout the Scottish Highlands. Dr. Cockayne points out to me that the descriptions of the larva given in the current text-books are in error: it is always green and feeds only upon Bearberry, *Arctostaphylos*.

The Scotch Annulet, *Gnophos obfuscaria*, Schiff., Selidosemidae, is a species of extensive distribution but only in the north, inhabiting moors on the lower slopes of mountains approximately from the Forth-Clyde isthmus. The larva feeds upon heath, ling, broom and Needle-furze, *Genista anglica*, and though the imago is well concealed when it rests with wings outspread upon rocks and stone walls, it much more frequently hides itself in holes or under projections.

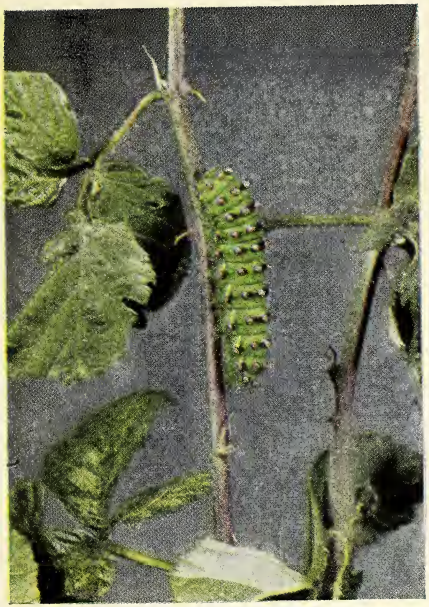
A number of other moths belong to what may be called the Arctic-Alpine group, being found only on Scotch mountains or in Ireland and having a distribution abroad of a corresponding kind: Scandinavia and the Alps, with a discontinuity between them widened progressively by less suitable conditions since the last Ice Age. A few of these species warrant special mention here. One of the most celebrated and beautiful of them is the Northern Dart, *Amathes alpicola* Zett., Caradrinidae, shown in its three principal forms on Plate 27 (figures 1 and 2 male and female from Shetland, 3 and 4 male and female of the rather slate-coloured race from Aviemore, Inverness, 5 and 6 male and female from Rannoch, Perthshire). The Perthshire specimens are also of a slaty-grey shade when fresh, but this tint soon fades in that race. The moth has even been taken in England, but not in Ireland though it may possibly occur there. It is a species of high mountains, at least on the mainland, where the larva feeds on Crowberry, *Empetrum*. It occupies approximately the same territory as the Black Mountain Moth, *Psodos coracina* Esp. Selidosemidae (Plate 27, figures 10 and 12). The males of that curious-looking blackish little insect fly actively in the sunshine, usually at elevations from 2,000 to 4,000 feet. At the same time the females may be found running like flies over the stones. This and the foregoing species are to be obtained commonly only in alternate seasons: the Northern Dart is at any rate commoner in the even years of the calendar and the Black Mountain Moth in the odd ones: a most extraordinary circumstance which certainly seems to be substantiated by extensive observations. That these northern and high mountain species should take two years to develop is quite natural, but that they should preponderantly all emerge in the same season is truly remarkable and not easy to interpret. The origin of such a cycle is mysterious and, once begun, one would have thought that it would soon have been broken down by specimens sometimes taking one and sometimes three seasons to reach maturity. Evidently some exceptional mechanism must be in operation to maintain it. H. B. D. Kettlewell suggests that this may be a balance between the parasites attacking the more mature larvae (shown on Plate 27, figure 7 *A. alpicola*, and figure 11 *coracina*), such that each is especially vulnerable to the attacks of those normally infesting the other. In this way, larvae of either species which took a year too short or too long to develop would be eliminated and the two balanced cycles preserved. Though a mere suggestion with no evidence to support it, it is inherently possible; for when the Bath White butterfly, ordinarily a rare migrant here, became common in the Falmouth district in 1946, it seems to have been eliminated by the parasites of our native Green-veined White, which attacked its larvae in preference to their normal host.

Some of these British Arctic-Alpines are wide-ranging yet maintained in their special haunts by ecological conditions of a more subtle kind than the mere localisation of their food-plants. An example is provided by the Slender-striped Rufous, *Coenocalpe lapidata* Hb., Hydriomenidae, which as a larva apparently feeds on buttercup and grasses. Yet it is very local, in Scotland and the northern half of Ireland, at elevations of about 300 to 1,000 feet. An instance of extremely confined distribution within the same ecological group of species is provided by the Mountain Burnet, *Zygaena exulans* Hoch. (Plate 27, figure 8). This insect is very thinly scaled, the specimen illustrated being perfectly fresh though looking as if worn. In Scotland the larva feeds almost entirely upon Crowberry, *Empetrum nigrum*, but abroad it eats various alpine plants, the Mossy Campion *Silene acaulis*, *Arenaria cherleria* and others. Evidently the food plant cannot account for the extreme localisation of this moth to a single mountain, with a higher and a lower summit, near Braemar (Map 7).

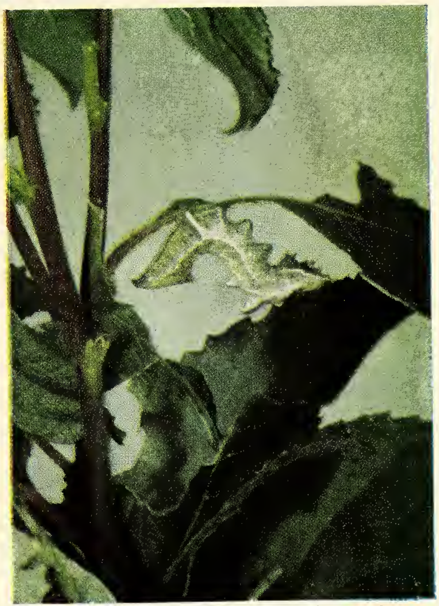
One other member of the Zygaenidae, the Oban Burnet, *Zygaena achilleae* Esp. (Plate 27, figure 9), found only in Scotland so far as the British Isles are concerned, is mentioned here merely as an illustrative contrast. For this is not an Ice Age relict at all but one of those species to which attention has several times been drawn, both in *Butterflies* and in the present volume, which survive at the extreme edge of their range by adjusting themselves to some special set of conditions; in this instance, those provided by the Oban district of the west coast of Scotland. For elsewhere the range of this moth gives no suggestion of an Arctic or Alpine habitat, since it is widespread in Central and Southern Europe, being a well-known insect of the Mediterranean coast and of Spain. It will be noticed that this is a very different type of distribution from that of the other species now under discussion. It probably reached this country during the particularly warm first interglacial phase of the last Pleistocene glaciation.

Those moths which combine northern and Alpine requirements with an exceedingly restricted distribution present an unsolved problem in ecology which it would be fascinating to investigate. One or two further instances may be given. The Rannoch Brindled Beauty, *Poecilopsis lapponaria* Bad. (Plate XIII, figures 3 and 5), Selidosemidae, seems to be confined to Perthshire, Inverness and Argyllshire, where it occurs in a few localised places, generally on boggy land near streams. Here the winged males and wingless females may be found in April and May resting on heath and bog myrtle, on which also the larva feeds; so that the insect is certainly not thus localised by its food-plants. A very similar problem is presented by that magnificent species the Rannoch Sprawler, *Brachionycha nubeculosa* Esp. (Plate 28), Caradrinidae. It feeds upon birch, but is not only a northern but an extremely localised moth. It was long thought to be restricted to the immediate neighbourhood of Rannoch in Perthshire, but is now known to occur also in Aviemore, Inverness, where the specimens are recognisably different from the much better-known Rannoch form (Figure 6), being paler and more strongly marked (figure 7). This is an early spring species which is to be found resting upon the trunks of birches and other trees growing with them, in late March and the beginning of April. It is quite possible therefore that its distribution in Scotland is much wider than is generally supposed. For those who collect at that season tend to go to places where this and other species are well known to occur, rather than to risk failure but perhaps gain far greater interest and information by sampling new ground. The Rannoch Sprawler is apt to remain in the pupal stage for one, two or three years: possibly a useful adaptation for a northern insect appearing so early in the year, as it will ensure that at least a proportion of the population would survive an exceptionally inclement season. Another of these curiously restricted northern insects is the Cousin German, *Triphaena sobrina* Gu., Caradrinidae. This is a typical Arctic-Alpine, whose distribution comprises Scandinavia, Northern Russia and the Alps. In Britain, however, it is apparently limited to a few districts in Perth and Aberdeen; but again it is probable that the full extent of its range is not known.

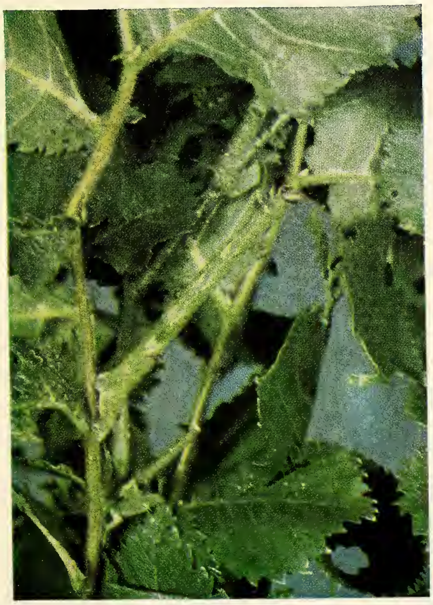
By no means all these Ice Age relicts are mountain moths. Some though confined to the far north require a low elevation. This is true of the Northern Argent-and-Sable, *Eulype subhastata* Nolcken, Hydriomenidae. It is widespread in Scotland, and has been taken even as far south as North Wales. The larva feeds upon sweet-gale and bilberry, whereas the closely allied Argent-and-Sable, *E. hastata* L., of which it was long thought to be a race, is restricted to birch and has a wide range throughout Southern Britain and Ireland. Similarly the Rannoch Looper, *Itama brunneata* Thnbg. (Plate 29, figure 11 Aberdeen and 12 Stafford), Selidosemidae, which occurs from Perthshire northwards, is not a mountain species. This moth, which feeds on bilberry, has a rather mysterious distribution since occasional specimens are



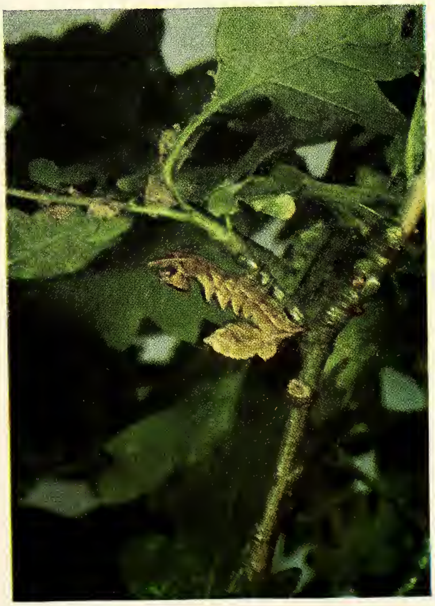
1. Emperor, *Saturnia pavonia*, fully grown



2. Pebble Prominent, *Notodonta ziczac*

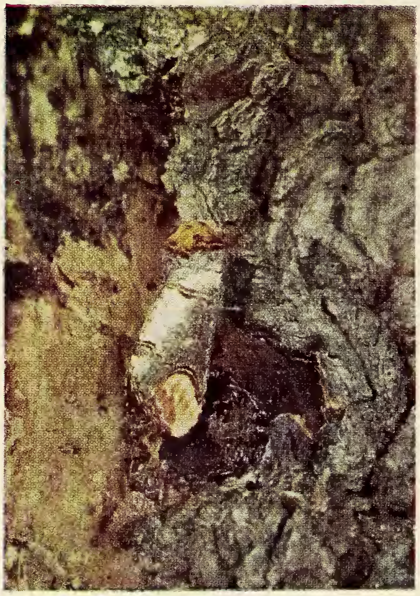


3. Peppered Moth, *Biston betularia*

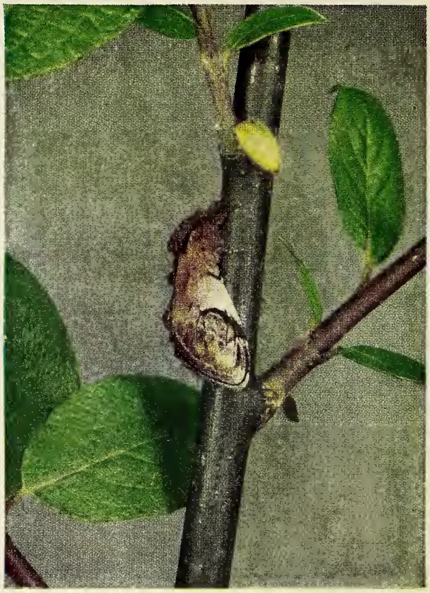


4. Lobster Moth, *Stauropus fagi*

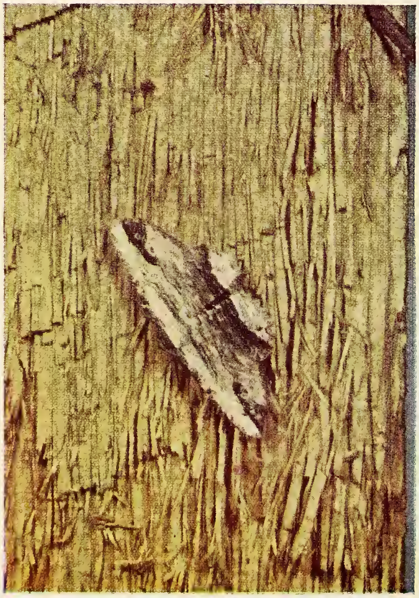
Plate 19. LARVAE



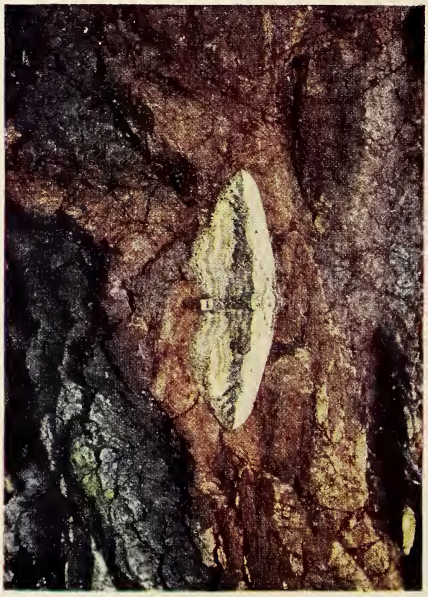
1. Buff-tip, *Phalera bucephala*



2. Pebble Prominent, *Notodonta ziczac*



3. Waved Umber, *Hemerophila abruptaria*



4. Small Waved Umber, *Horisme vitalbata*

Plate 20. RESEMBLANCES TO BARK AND WOOD

taken in England, but always as extreme rarities; one of them is illustrated on the Plate. It is just possible that, as the insect moved northwards, a few struggling colonies were left behind in which the species survived, in small numbers only, in habitats unsuitable to it and to which it failed properly to adjust itself. However, it is far more likely that these southern specimens are the descendants of recent immigrants.

It is, of course, to be expected that certain of these Arctic-Alpines, with somewhat greater tolerance, would succeed in maintaining themselves in Northern England as well as in Scotland. Thus the Grey Mountain Carpet, *Entephria caesiata* Schiff., Hydriomenidae, is to be found on mountains and high moorlands in the north of England and throughout Scotland, including Shetland: it is also widespread in Ireland (Map 2). The larva feeds upon bilberry, heather and ling, and the imagines habitually rest upon rocks and stone walls and are then extremely difficult to detect. In its appropriate haunts several specimens will often take to the wing if a handful of small stones be thrown against a rock-face in late June and July. The closely allied Yellow-ringed Carpet, *E. flavicinctata* Hb., is more decidedly an insect of the north and the mountains. In England it is common but very local in Yorkshire and scarce in the Lake District. It does not become frequent in Scotland until the highland zone, where it is generally plentiful. It is also found in Northern Ireland. Its food-plants are also more decisively alpine in character, consisting of mountain saxifrages (see page 184). The moth much resembles the Grey Mountain Carpet, but there is a scattering of yellowish scales upon the fore-wings which give it the appearance of one of the more orange lichens when at rest. It is much the more difficult both to see and to disturb.

Another decisively Arctic-Alpine insect is the Manchester Treble-bar, *Carsia sororiata* Hb., Hydriomenidae, which feeds upon Cowberry, *Vaccinium vitis-idaea*, and Cranberry, *V. oxycoccos*. Thus it is limited to heaths and moors. It is found from Northern England through Scotland to the Shetlands, and is rare and local in Northern Ireland.

Quite a number of moorland species found in Scotland and the north of England penetrate as far south as Staffordshire. Among these may be mentioned the Golden-rod Brindle, *Lithomoia solidaginis* Hb., Caradrinidae, the Scarce Silver-Y, *Plusia interrogationis* L., Plusiidae, and the Small Autumnal Carpet, *Oporinia filigrammaria* H.-S., Hydriomenidae, an insect peculiar to the British Isles. This belongs to a genus of closely allied species, and it may well have evolved from the Autumnal Moth, *O. autumnata* Bork., as an adjustment to moorland conditions. It feeds as a larva upon heather and bilberry. Both the Small Autumnal Carpet and the Scarce Silver Y are found also in Ireland. As is to be expected, several species having this type of distribution, but more definitely associated with high ground, spread also to Wales. The Chestnut-coloured Carpet, *Thera cognata* Thnbg., Hydriomenidae, is one of them, its distribution being dependent upon that of its larval food plant, the juniper. However, it does not follow this into Southern England as does the Juniper Carpet, *T. juniperata* L., Hydriomenidae (page 141).

Interglacial Relicts

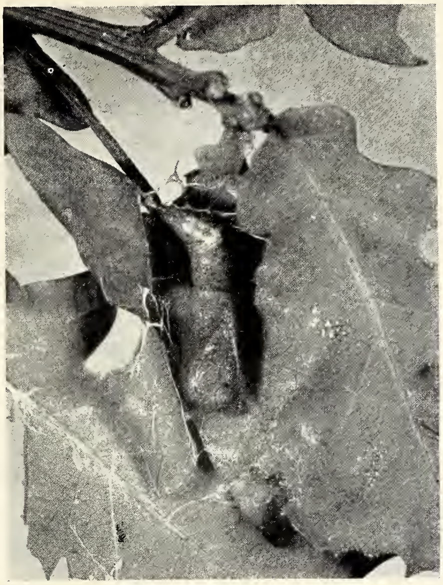
The insects so far mentioned in this chapter appear to be relicts from the glacial phases but, as already suggested, survivors from interglacial conditions seem to exist in South-west England, some parts of the West coast of Britain and in Ireland. Several species with a range abroad entirely different from that of the Arctic-Alpines are wholly confined to the Dumnonian Peninsula. Now these must be carefully distinguished from migrants which sometimes succeed in establishing an impermanent colony here, for several migration-routes pass through Devon and Cornwall (see Chapter 6). However, such a species as the Scarce Blackneck, *Ophiusa craccae* Schiff., Plusiidae, appears to be an established native, since it is found in many places along the rocky north coast of both counties, the larva feeding on wood-vetch. As it occurs nowhere else in Britain, so far as is known, it is likely to be an interglacial relict which has maintained itself in this favoured corner of England, which remained relatively far from the ice. The evidence against migration and in favour of survival is, however, more complete in respect of two other species, both Caradrinidae, and almost restricted so far as Britain is concerned to the south-west; for one of them, Barrett's Marbled Coronet, *Hadena barrettii* Dbl., extends north to Anglesey and occurs in Ireland (see page 131), while the other, the Black-banded, *Antitype xanthomista* Hb., is an inhabitant also of the Isle of Man; moreover, the British race differs from any form on the Continent. This latter species is confined to the rocky parts of the coast, where the larva feeds upon plantain and the flowers of the Wardrobe-plant or Sea-thrift, *Armeria maritima* (Map 5).

It might reasonably be anticipated that the Isles of Scilly, which enjoy by far the most favoured climate in Britain and support an otherwise Mediterranean Insectivore, *Crocidura*, found nowhere else in Northern Europe, might have preserved several interglacial species of moths. But it seems that this hope is not to be realised, for the Lepidoptera of this archipelago are now fairly well known, and no species absent from the British mainland has been obtained here. The two specimens of *Cosymbia pupillaria* (Plate 29, figure 2), Sterrhidae, found in Scilly must almost certainly be migrants, or more probably casual introductions among foreign plants brought to the sub-tropical gardens so long and successfully maintained at Tresco Abbey by the Dorrien-Smith family. Three other examples of it have been taken in the south of England. In company with my colleague, W. H. Dowdeswell, I have a somewhat extensive personal experience of the entomology of these islands, but our work there has involved mathematical and ecological studies; we have not been engaged in ascertaining their fauna. However, our general acquaintance with them leads me to think that the rather uniform character and the small size of these islands have prevented them from acting as a haven of refuge for moths otherwise obliterated from Britain. The only exception I would be inclined to make to this statement, and that tentatively, is the existence there of an unexpected species, the Kent Black Arches, *Nola albula* Schiff., Nolidae. Elsewhere it is established in Kent, Sussex and the Isle of Wight which, like so many other post-glacial colonists, it probably reached across the Dover-Calais land-bridge, or subsequently by migration. The fact that this insect is not known along the north coast of France is hardly relevant for it is easily overlooked, nor does its small size and the distance across the Channel exclude it as a migrant: still smaller moths (such as the three species of the genus *Eublemma*, Plusiidae, occasionally reported here) reached Devon by that means. On the Continent, the Kent Black Arches feeds upon bramble, cinquefoil and other plants, but in England upon dewberry, and it seems at least possible that it exists in Scilly as an interglacial relict.

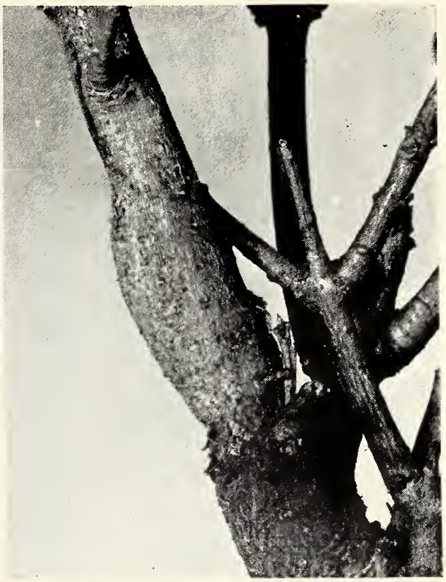
We have here at least a suggestion that the discontinuous distribution of a species, Scilly and Kent, is due respectively to survival from an interglacial phase and to repopulation in Holocene times. This must also be the explanation of the extraordinary range of the Least Carpet, *Sterrha rusticata* Schiff., which in Britain is to be found only on the island of St. Kilda and in scattered localities along the south coast of England: Torquay, Portland and East Kent.

An instance of what is apparently an interglacial relict is provided by the Frosted Yellow, *Isturgia limbaria* F. (Plate 29), Selidosemidae. The larva of this moth feeds only upon Broom, *Cytisus scoparius.* The imago rests with the wings closed above the back, and the cryptic colouring of the underside makes it inconspicuous when sitting upon this plant (figure 14). Though the species was in former times reported from Kent, it was long supposed to be restricted to the Ipswich district of Suffolk; but even there it has apparently been extinct for the last forty years or so. However, a little-known race exists also in the north-west of Scotland. The area has been but imperfectly explored entomologically, and very few specimens have so far been taken. One of them is shown in Plate 29, figure 15. They are slightly larger and paler than the English race (figures 13 and 14). This insect has apparently survived the glacial phases in the North Sea—East Anglia area; also off the west coast of Scotland (page 151), whence, with the increasing warmth since the retreat of the ice, it has extended back into the valleys of Ross-shire.

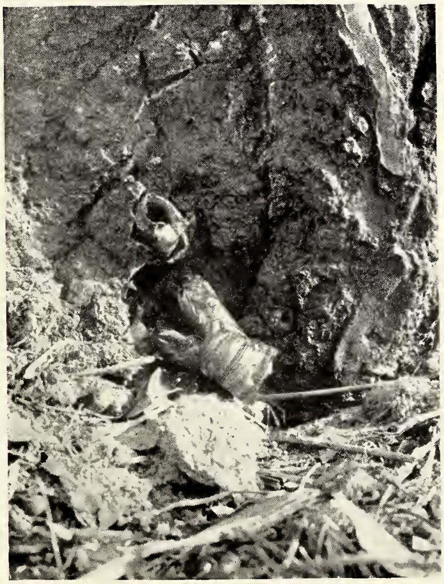
It has been suggested that some species have survived the glacial phases on the now submerged low-lying land surrounding Wales. It seems probable that the colony of Guenée's Rustic, *Luperina nickerlii* Frey, Caradrinidae, which until 1921 existed at St. Anne's-on-Sea on the Lancashire coast, may have been a relict of this kind. It is true that its known history here is extremely short, for it was first recorded only in 1909; but the moth had exceptional habits and, seldom flying, required searching for, while the colony was as large when first discovered as subsequently. There is no reason to suppose that it was not native there. Its restricted locality in Lancashire was destroyed by urbanisation. However, three specimens were caught in North Wales about 1860, and Dr. Cockayne informs me that he has reason to believe that it still exists there. The British form is either specifically distinct or a subspecies of the Continental *L. gueneei*, so it did not reach Lancashire as a chance importation; indeed, it is an insect most unlikely to be accidentally introduced. The claim of the area surrounding the Welsh coast to support interglacial relicts could be sustained with varying degrees of probability by reference to a number of species.



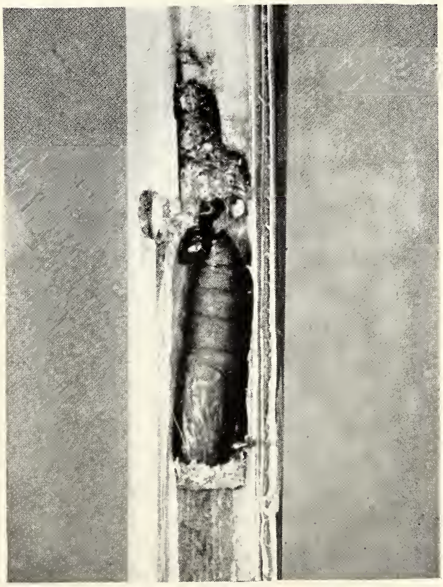
1. Large Thorn, *Ennomos autumnaria* (X 1.25)



2. Waved Umber, *Hemerophila abruptaria* (X 1.25)

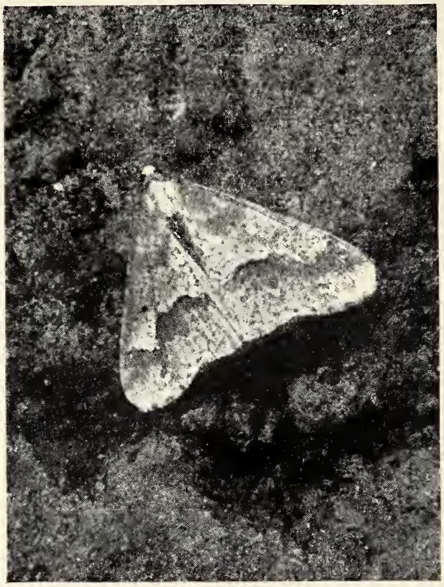


3. Hornet Moth, *Sesia apiformis*, after emergence of moth (X 1.25)

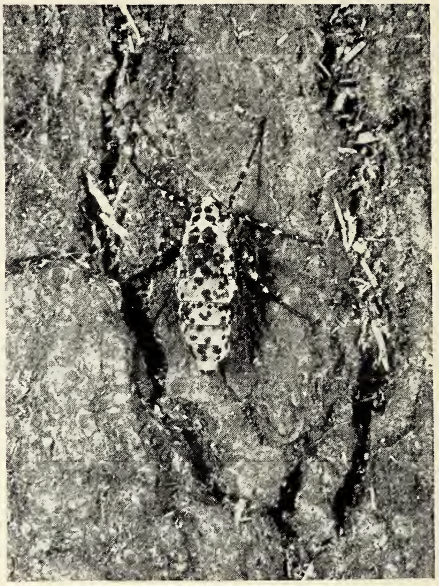


4. Bulrush Moth, *Nonagria typhae* (X 1.25)

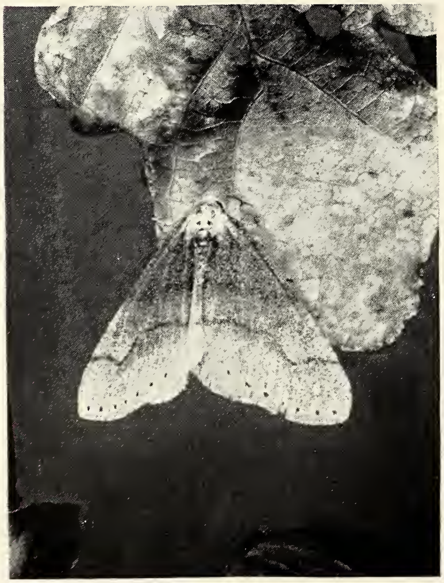
Plate XVII. PUPAE



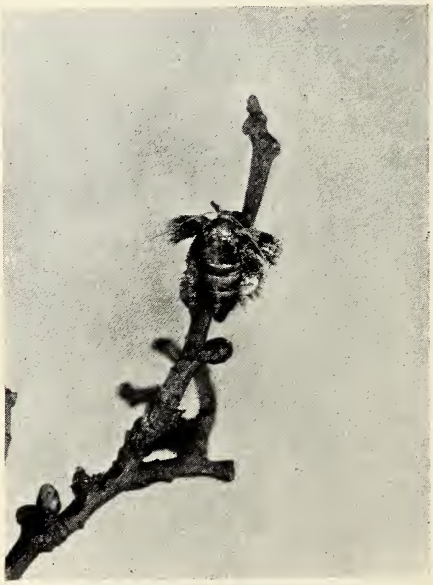
1. Mottled Umber, *Erannis defoliaria*, male (X 1.5)



2. Mottled Umber, *Erannis defoliaria*, female (X 2)



3. Dotted Border, *Erannis progemmaria*, male (X 2)



4. Dotted Border, *Erannis progemmaria*, female (X 2)

Plate XVIII. MOTHS WITH WINGLESS FEMALES

Doubtless most of them would be obliterated as the sea rose, but some would obtain a foothold on the surrounding land as this became warmer. Ashworth's Rustic, *Amathes ashworthii* Dbl. (Plate 26, figure 3), Caradrinidae, and Weaver's Wave, *Sterrha eburnata* Wocke (Plate 26, figure 5), Sterrhidae, both of them entirely restricted to North Wales as far as the British Isles are concerned (see page 122), are certainly examples of such insects.

Two moths have survived not only there but in two more of the regions mentioned on pages 150-1 as having provided refuges for interglacial forms: the Western Isles of Scotland and the west coast of Ireland. The first of these is the Belted Beauty, *Nyssia zonaria* Schiff. (Plate XIII, figure 4 winged male and 7 wingless female), Selidosemidae. This has a remarkable discontinuous distribution, for it is found along the sandy coasts of North Wales and South Lancashire, on a number of the islands in both the Inner and Outer Hebrides, and at various places on the coasts of Antrim, Mayo and Galway in Ireland. The larval food is mainly Bird's-foot trefoil, *Lotus corniculatus*, dock, dandelion and a number of other common plants. The second is the Transparent Burnet, *Zygaena purpuralis* Bruennich, which is extremely distinct from the classificatory point of view, yet its singular range of localities bears so strong a resemblance to that of the last species as hardly to be due to coincidence. For it also is found at Abersoch in North Wales; on the west coast of Scotland, where it is established in the Oban District and in the islands of Gunna, close to Coll, and Rhum (Inner Hebrides)*; in addition, it occurs on the west coast of Ireland (Map 6). The Rhum locality on the south side of the island is shown in Plate XXII, being a photograph kindly taken for me by Mr. J. L. Campbell of Canna. This consists of rough ground at the foot of precipices so steep as to make it inaccessible from the land. It can only be reached by boat, and this indeed is a hazardous proceeding not to be attempted save in calm weather. Here on the broken ground between the cliffs and the sea this Burnet is to be found abundantly. In Ireland its habitat is the Burren of County Clare, an extraordinary district to be described on pp. 165-6.

*There is a rumour that a colony of this insect exists, or existed, on the east coast of Scotland. It is hardly appropriate to consider its significance until this has been verified.

IRISH LEPIDOPTERA

When we turn our attention to Ireland itself we find there many striking interglacial relicts, both plants and animals, especially of course in the south-west. Among plants, the Strawberry Tree, *Arbutus unedo*, the Mediterranean Heath, *Erica mediterranea*, and the London Pride, *Saxifraga umbrosa*, and among animals the Spotted Slug, *Geomalacus maculosus*, are famous examples of Mediterranean forms which have survived there alone in Northern Europe. They are remnants of the fauna which colonised the low-lying country between Ireland, Northern France and Spain, to which reference has already been made on page 150.

Unfortunately our information on Irish moths is scanty. The poor communications and great extent of moorland, bog and mountain, have made it difficult to study them, while there have never been many resident entomologists in that country. Moreover, the history of the subject has not been altogether fortunate, for a number of the older records are undoubtedly incorrect or even falsified. However, such spectacular discoveries have been made in recent years that some of those long regarded as inadmissible may yet be verified. Here it is only necessary to draw attention to a few characteristics of the Irish moths, and to one or two of the most remarkable and recent additions to the list of them, in order to indicate that results of importance are to be anticipated from a more thorough entomological survey of that country.

I should make it clear that throughout this book the term Ireland is used purely in its geographical sense, as one of the British Isles. The political concepts of Eire and Northern Ireland are meaningless from a scientific point of view, as these countries have no natural boundaries.

The Silver Barred, *Eustrotia olivana* Schiff., Plusiidae, is an example of a moth which survived the glacial phase in two regions: South-west Ireland, and the submerged land to the south of it, and in the East Anglian and North Sea area (page 151). For in the British Isles it occurs in two Fens in Cambridgeshire, though it was formerly found in Norfolk, and in Kerry where it is local (Map 3). The Irish specimens are on the average slightly more reddish than the English, but the character is not an absolute one.

It is doubtful how much light is to be thrown upon our relict moths by a study of the Marbled Green, *Cryphia muralis* Fors., Caradrinidae. This is normally a coastal species and several forms of it are known, but their nomenclature is in some confusion. Typical *muralis* seems to be a grey-green insect with the fore-wing markings distinctly outlined in black, while *par* is yellowish-green and without the black edging to the pattern. Certainly *muralis* and *par* occur together throughout the wide distribution of this species in the coastal districts of Southern England as well as of Ireland. There is also a very distinct black and white form, *impar*, so far found only in the towns of Cambridge and Gloucester. It has been recorded from Ireland, but Dr. Cockayne informs me that the specimens from that country are distinct. It seems then that a variety of this insect has been able to adjust itself to the conditions of these towns, which provide an unusual type of locality for it. The species is probably an Ice Age relict in Ireland while its status in England is doubtful, though it may have survived a glacial phase there, in the Channel and North Sea areas.

Another moth which exists both in south-west Ireland and in Southern England is the Bordered Gothic, *Heliophobus reticulatus* De V., Caradrinidae. The long separation of this insect in these two areas is attested by the fact that the English specimens are unlike any others, while the Irish race resembles some of those found on the Continent.

The Muslin Moth, *Cycnia mendica* Cl., Arctiidae (Plate 10), is an interglacial relict in Ireland. Normally, as in Britain, this is a species with extreme sexual dimorphism, the males being blackish (figure 7) and the females white with black dots (figure 8). However, in Hungary, Rumania and some other places in South-east Europe, the ordinary *mendica* is replaced by *rustica* in which the males are much like the females, being white, cream-coloured (figure 9) or occasionally ochreous-brown, and this is the race which occurs exclusively in Ireland: the females of true *mendica* and of *rustica* are not distinguishable. The genetics of these two forms will be discussed on pages 176-7.

On the other hand, the Scarce Silver-Y, *Plusia interrogationis* L., is one of the northern types which survives in Ireland. It has been sufficiently long isolated there to become recognisably distinguishable from the British form, the specimens being distinctly flushed with red. Haworth's Minor, *Celaena haworthii* Curt., Caradrinidae, probably belongs to the same ecological group and has become widespread in the north of the country. Except for some records from Killarney and from the Dorset heaths in England, it has failed to establish itself in the south; however, it is not uncommon in Norfolk. Other Arctic-Alpine moths which have reached Ireland are mentioned on pages 157-8, and there are a number more of them.

The possibility that very unexpected species survive in Ireland from the first interglacial phase of the last Ice Age has been suggested by various unconfirmed reports, but those of the Hon. R. E. Dillon must be disregarded. Some of the remainder are doubtless due to error but others are reliable, among them the capture of a Bloxworth Snout, *Hypena obsitalis* Hb., Plusiidae, which was taken at Ivy Bloom in October 1936 at Ummera, County Cork. There is no question of either the identity or the authenticity of this specimen. It is the third ever recorded in the British Isles, the other two having been caught respectively in South Devon and Dorset. Its occurrence must either indicate its existence as an unsuspected native in Ireland, which is not an impossibility, or an extraordinary act of migration. The latter alternative is somewhat strengthened by the fact that it was found with nine specimens of the Gem, *Nycterosea obstipata* F. (Plate xx, figure 6 male, 7 female), Hydriomenidae, which is a migrant species in England, though perhaps it may be a resident in Ireland.

It is now certain that the White Prominent, *Leucodonta bicoloria* Schiff., Notodontidae, at one time considered an almost fabulously rare insect in these islands, is established over a wide area in south-west Ireland, though it is difficult to find. This is a white moth marked with orange, very dissimilar in appearance from the other British species of its family. Its English history began with the capture of a specimen in the Burnt Woods, Staffordshire, in 1861. A few more were taken there, but none is known to have been seen in that locality for eighty years and, except for the record of one or two caught on the south coast, probably immigrants, this completes its history in Britain. In Ireland it was discovered in 1859 in Killarney. Several more were taken during the next ten years, after which only two or three specimens were found until Col. C. Donovan discovered the larva in 1932 by beating birches in the Kenmare river basin. He next obtained eighteen larvae near Killarney, but though one or two others have been found, no further information on this moth has been brought to light during the last few years; probably because insufficient search has been made for it owing to the small amount of collecting done in Ireland.

The most recent event in the history of Irish Lepidoptera is the spectacular discovery that the moth *Calamia virens* L., Caradrinidae, is an established resident in the Burren district of County Clare. This is an extraordinary region in the north-west of the county, bounded on its northern side by Galway Bay. It is formed of limestone hills rising to over 1,000 feet, from which the surface soil has been eroded. The resulting ground consists of vast rock platforms intersected by deep slits and crevices. At the higher levels it appears destitute of life, and nothing but the bare rock is to be seen. Yet a closer inspection shows that the cracks and channels contain a rich assortment of plants, including many rare species for which the Burren has long been famous. At lower elevations an abundant hazel scrub grows from the crevices.

In August 1949 Mr. W. S. Wright, who was studying the botany of the region, found a large green moth unfamiliar to him at rest on bracken. This proved to be *C. virens*, a species never before reported in the British Isles and unlike any other occurring here. It is about 1½ inches across the expanded wings. The front pair are bright green with two small white dots, and the thorax is green also; the abdomen and hind-wings are white in the female but slightly smoky in the male. In a fresh specimen the fringes and legs have a pinkish tinge.

It is said that the species fades badly in collections. I do not know if the green colouring be of the type which is changed to brown by acids, as in the Geometridae, the ‘ Emerald Moths,’ or by alkalis as in the green Cymbidae, the ‘ Green Silver Lines ’ and allied species (see page 6), and this should be determined. If the latter alternative be correct, as I suspect, it is possible that the colour of faded specimens could be restored by placing them in an atmosphere containing dilute hydrochloric acid.

It was rightly felt that this discovery required full investigation; especially as the species has a very different habitat abroad, being found on sand hills. Consequently, in 1950 a party of entomologists visited the Burren, and by the use of powerful mercury-vapour lamps proved that it is actually common in some parts of the region. They found a specimen drying its wings and succeeded in digging up the empty pupa-case. Since then several pupae have been obtained and it has been established that the larval food-plant is a grass, *Sesleria*, confined to the Burren and to a small area in North-west Yorkshire. Once one of the breeding places has been discovered, dozens of the moths may be seen resting on the grass and drying their wings.

The entomologists who visited the Burren in 1950 also found established there a new form of the Straw Belle, *Crocota gilvaria*, Schiff., Selidosemidae, in which the normally straw-coloured wings are dusted with grey scales. The species has heretofore been rare and little-known in Ireland. This is also the Irish locality for the Least Minor, *Phothedes captiuncula* Treits, Caradrinidae. It exists there in the form *tincta*; this is distinct from that occurring in England, where it has a curious north-country range including Northumberland, Durham, Westmorland and Lancashire. It is extremely local in these counties. In Ireland it is presumably an interglacial relict. In England it has adjusted itself to very different conditions, its colour-pattern being altered in the process. The Burren is also, as already indicated, the locality for the Irish form of the Transparent Burnet.

The discovery of *Calamia virens* in County Clare (Map 7) suggests that entomological treasures await further search in Ireland, and the history of that country in the late Pleistocene indicates that it may support further traces of a Mediterranean fauna, survivals from the interglacial phases. A thorough investigation of the moths of the Burren is clearly necessary, but it must be stressed once again that what is wanted is entomological *exploration*: in order to obtain the information that is needed, collectors would have to resist the temptation to visit the few celebrated localities where unusual species are known to occur. Even the history of the Burren itself is an object-lesson in the evil of collecting Lepidoptera rather than studying their natural history. For the area is quite well known to entomologists, who have in the past gone there in late June and early July to obtain specimens of the Transparent Burnet. Consequently, they failed to appreciate its unusual entomological possibilities. Thus it was not even realised that one Irish butterfly, the Pearl-bordered Fritillary, *Argynnis euphrosyne* L., is to be found in that locality alone. Because this is on the wing in May and early June it was not detected until 1922, while the recent discoveries in the Burren have necessitated both day and night work during August. Yet an ecologist could have seen that this district, already famous for the strange and rare plants which it harbours, was the very one to repay thorough entomological investigation throughout the season.

Relicts and Holocene Colonists

It will be realised then that our relict moths consist partly of Arctic-Alpine species, which survive in the northern part of Britain and sometimes on mountains farther south. Some of them crossed overland into Ireland and there they have maintained themselves chiefly in the north, but have to some extent extended their range southwards by adjustment. In addition, we possess traces of a more Mediterranean fauna which has lingered on from the interglacial phases in and near favoured places (pages 150-1). Their distribution distinguishes such species from those which maintain themselves as migrants and sometimes establish populations in this country which survive for a number of generations but not permanently (Chapters 6 and 10), and also from the great mass of Holocene colonists. These latter, arriving in the south, generally the south-east, have often spread up Britain, becoming rarer in the north-west. Examples of them are the Cream-spot Tiger, *Arctia villica* L., Arctiidae (Map 12), and the Oak Hook-tip, *Drepana binaria* Hufn., Drepanidae (Map 11). Others have got no farther than the south-eastern corner of England, where they have been able to adjust themselves to restricted conditions which do not differ greatly from those on the opposite side of the Channel. Instances of such species are provided by the recent remarkable discoveries in the woods of the Ham Street area of Southern Kent, where it seems that several moths thought to be very rare, or merely casual immigrants to this country, are in fact residents (pages 147-8). These include the Clifden Nonpareil, *Catocala fraxini* L., and the Lunar Double-stripe, *Phoberia lunaris* Schiff., both Plusiidae. The latter species is also established in a few other situations in south Kent and in mid-Sussex, and there seems to be just a possibility that it also exists as an interglacial relict in Ireland. It will be noticed that the extremely restricted range of these insects in south-eastern England is in striking contrast with that of the interglacial relicts wherever they may have survived.

Quite a number of moths have a rather anomalous distribution, being restricted in Britain to southern and especially south-eastern England but occurring also in Ireland. The Scarce Footman, *Eilema complana* L., Arctiidae, the Square Spot, *Ectropis consonaria* Hb., Selidosemidae, and the Lackey, *Malacosoma neustria* L., Lasiocampidae, are examples of them. It is likely that the majority of these represent a double colonisation of the British Isles: the Irish specimens being interglacial relicts and the English ones Holocene arrivals. Alternatively, the English specimens may have survived a glacial phase in the extreme south in the area covered by the English Channel, from which they spread some way northwards with the retreat of the ice. It is, of course, possible that some of these species may formerly have occurred much more widely, including Western Scotland in their range, and that they crossed to Ireland before the land-connection with that country was severed. They may subsequently have died out in the north of England and Scotland if their survival were more precarious there.

The last land-bridge between Ireland and Britain did not close what is now the narrowest gap between them, at the north-east corner of Ireland, but sloped northwards from the Inishowen Peninsula, along the north coast of that country, to the Inner Hebrides, so that the Western Isles of Scotland are near the site of this connection. J. W. Heslop Harrison has drawn attention to the Irish affinities to certain of these islands, in particular, Coll and Tiree. To Coll must be added the little island of Gunna, separated from it only by a few hundred yards. Between them, these two contain a curious assortment of otherwise Irish plants and insects, a number of which are unknown on the Scottish mainland. The plants important in this connection are *Sisyrinchium*, the orchid *Spiranthes romanzoffiana*, and the Pipe-wort *Eriocaulon*; while among the insects may be mentioned the Marsh Fritillary butterfly, *Euphydryas aurinia* Rott., which exists there in its Irish race *praeclara*, the Transparent Burnet, the Belted Beauty Moth and the humble-bee, *Bombus smithianus*. The existence of the two latter species on Rhum, where the Transparent Burnet also occurs, on Tiree and on some of the Outer Isles suggests, as Harrison claims, that these islands, as well as Coll and Gunna, situated at or near the northern end of the last land-bridge to Ireland, remained in connection with the latter country after their separation from the Scottish mainland.

Plate XIX. 1 (*above*). The Chilterns: The habitat of numerous Chalk Down species
2 (*below*). Cothill, Berkshire: Where the Scarlet Tiger has been studied experimentally

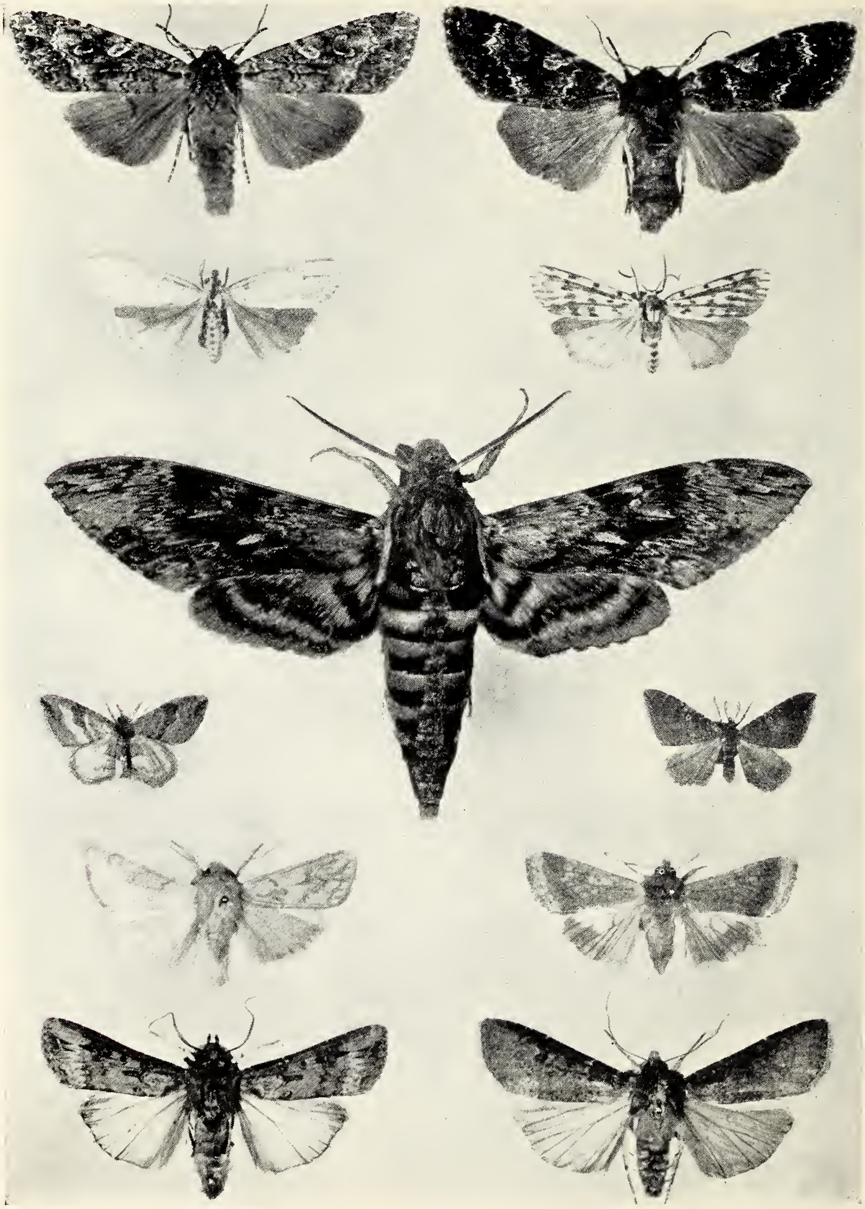


Plate XX

Plate XX. MIGRANTS

1
RANNOCH

2
ESSEX

3
' ENGLAND '

4
BOURNEMOUTH

5
TORQUAY

6
Male
S. DEVON

7
Female
S. DEVON

8
S. DEVON

9
S. DEVON

10
CUMBERLAND

11
DORSET

---

1. and 2. Great Brocade, *Eurois occulta;* 3 and 4. Speckled Footman, *Coscinia cribrum;* 5. Convolvulus Hawk, *Herse convolvuli;* 6 and 7. The Gem, *Nycterosea obstipata;* 8. The Delicate, *Leucania vitellina;* 9. Scarce Bordered Straw, *Heliothis armigera;* 10. Dark Sword Grass, *Agrotis ypsilon;* 11. Pearly Underwing, *Peridroma saucia*

CHAPTER 12

GEOGRAPHICAL RACES

ISOLATION AND VARIATION

THIS CHAPTER is devoted to a study of geographical variation illustrated by means of British moths. Some aspects of that subject have already been considered in relation to Polymorphism and Relict Faunas, and these will not again be touched upon unless to illuminate them from a different point of view. The races chosen for discussion are classified on the basis of ecology and evolution, a procedure frequently adopted in other groups of organisms but unfamiliar in accounts of Lepidoptera, except that it has to some extent been used in the previous volume of this work.

This is rather a disappointing branch of entomology. One might have hoped that a considerable body of information both on the genetics and ecology of the geographical races of the Lepidoptera would by now have accumulated; but in spite, or because, of the immense amount of collecting which has been done in this Order, greater certainly than in any other, our information on these subjects is scanty. For instance, it compares unfavourably with what is known in birds and in many groups of plants. Thus it will here be possible to draw attention only to a limited number of examples which seem to provide particularly suitable material for such work, in the hope that they may be used in the future, and to review the few instances in which steps towards analysing this type of variation have already been taken.

As stressed by Ernst Mayr (1947), I believe with justice, isolation is essential for the formation of clear-cut geographical races or subspecies; though they may subsequently extend their ranges and meet (pages 181-2). Granted its existence, selection can act upon them to adjust them to their respective environments; a process which may or may not involve changes in the visible characteristics of the organism, depending on whether these are themselves being perfected in different directions, as often with cryptic coloration or, if not, whether they are detectably affected by the other adjustments which the insects undergo.

Various distinct situations may arise in the absence of isolation. Some species show an extraordinary degree of variability in both colour and marking throughout the whole of a more or less continuous range. The Common Rustic, *Celaena secalis* L., and the Clouded Drab, *Orthosia incerta* Hufn., both Caradrinidae, are examples of this; so is the July Highflyer, *Hydriomena furcata* Thnbg., Hydriomenidae. The first two are nocturnal and hide during the day, while the last is largely day-flying among such mixed foliage that it does not depend upon precisely adjusted colouring for concealment. In such circumstances, however, the colour-pattern may, but does not necessarily, become an indication of the vast potential variability of the organism, both genetic and environmental.

On the other hand, many physiological characters must be regulated with great exactitude, and in the species in which the necessary control affects also the superficial colouring this may be standardised to a surprising degree, provided that one of two conditions be observed. It may be immaterial to the preservation of the insect, as in a form hiding in crevices or among dead leaves and litter during the day. This is illustrated by the Flame Shoulder, *Ochropleura plecta* L., Caradrinidae, which has these habits. Though an abundant and uniformly distributed species, it is almost completely constant in appearance. So too is the Small Angle Shades, *Euplexia lucipara* L., Caradrinidae, also a common species, and many similar instances might be quoted. Alternatively, the colour-pattern may have achieved an effect useful in a wide range of circumstances. Thus samples of the Mother Shipton, *Euclidimera mi* Cl., Plusiidae, captured high on the chalk downs of southern England and in marshes in Cumberland are identical. So too are specimens of the Portland Moth, *Actebia praecox* L. (Plate 1), Caradrinidae, taken anywhere round our coasts, and it will be seen that their marbled greenish hue will render them inconspicuous on many types of herbage.

Clines

When, on the other hand, an organism which is not subdivided into distinct populations by isolation adjusts itself to its environment, a *cline** is formed: that is to say, a gradient in one or more characters as we pass from one type of habitat or climate to another. This may change quite slowly if the transition be gradual, but relatively sharply if it be abrupt. Evidently the extent of a cline will depend also upon the mobility of the species involved. In England the Autumnal Rustic, *Amathes glareosa* Esp., Caradrinidae, is of a pale soft grey coloration often with a pink flush. Passing north through Scotland it becomes darker and duller, while in Shetland it is deep grey but blackish on the west coast. Similarly in England the Northern Spinach, *Lygris populata* L., Hydriomenidae, a moth belonging to a very different group, has yellow fore-wings and white hind-wings. However, they become gradually suffused with brown through Scotland until in the Highland region the fore-wings are of a chocolate shade and the hind-wings dusky, though lighter forms are mixed with them, while on the mountains of the far north nearly black specimens occur. Here we have two instances of a gradual cline. Doubtless the variation involved is multifactorial, but it has never been studied genetically.

It sometimes happens that a cline continues on either side of a geographical barrier which isolates species into two populations which in other respects may or may not have evolved in different directions. This may occur when the climatic or other gradient responsible for the cline is maintained across the region from which the species is absent. For example, the ground-colour of the Grey Arches, *Polia nebulosa* Hufn., Caradrinidae, which is dusky grey in Eastern England, grows lighter towards the west until it becomes whitish in Ireland.

The development of a continuous cline depends upon adjustment to local conditions without geographical isolation: if discontinuous, this statement applies to each of its sections. Consequently, a different gene-complex must be built up along its length, mere distance supplying the isolation that is necessary. It is clearly possible, therefore, that the opposite end of a long though continuous cline may be sufficiently distinct to have sub-speciated, merely because genes do not trickle through the population fast enough to keep the adjustment, upon which the sexual balance depends, uniform throughout. Such a situation has several times been encountered, but I must illustrate it here from some breeding experiments of my own upon a butterfly, as I am not aware of any corresponding work upon a British moth.

The Large Heath, *Coenonympha tullia* Müller (Butterflies, Plates 42

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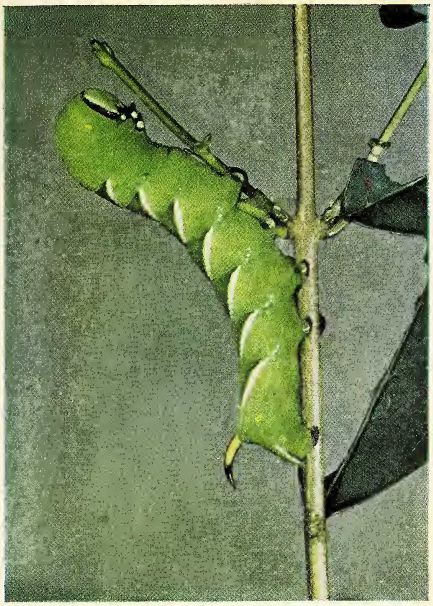
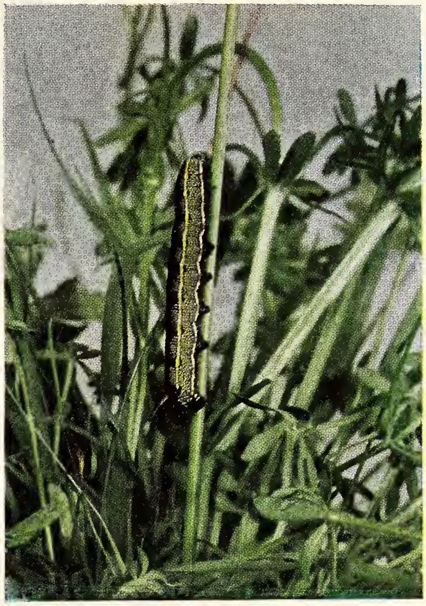
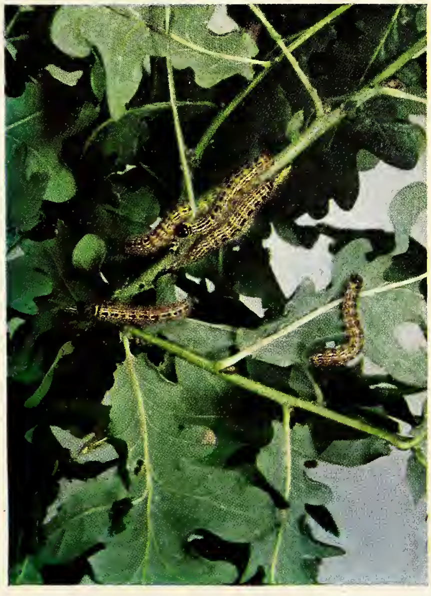
*A useful term coined by Julian Huxley (1939).



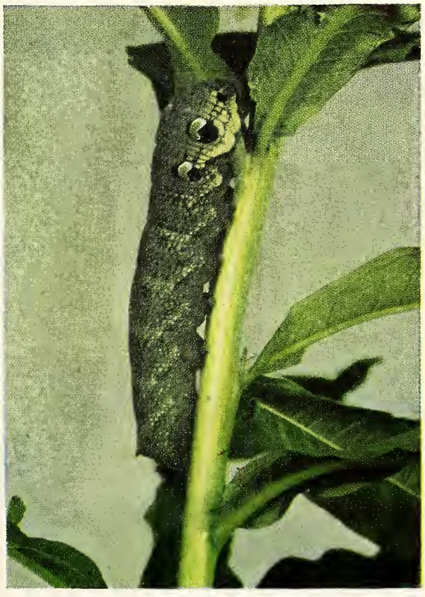
1. Privet Hawk, *Sphinx ligustri*



2. Striped Hawk, *Celerio livornica*

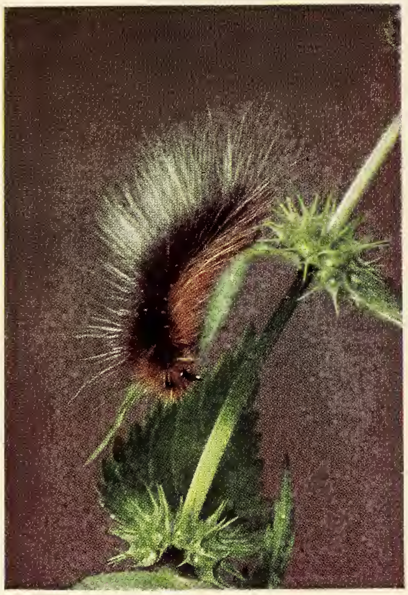


3. Buff-tip, *Phalera bucephala*, half-grown

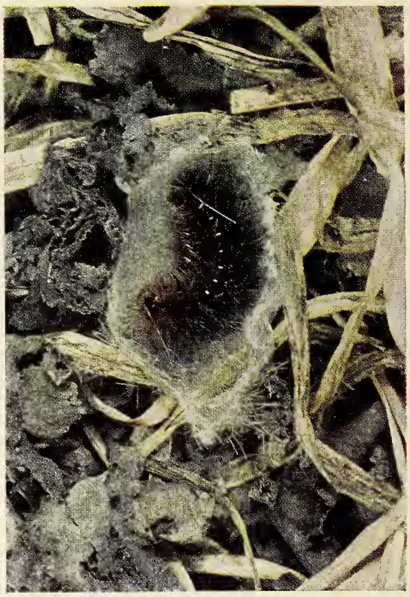


4. Elephant Hawk, *Deilephila elpenor*

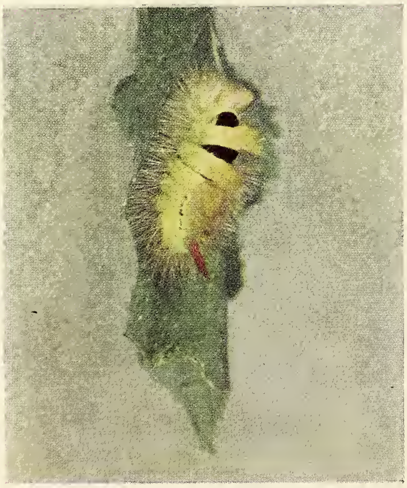
Plate 21. LARVAE: DISRUPTIVE AND WARNING COLOURS



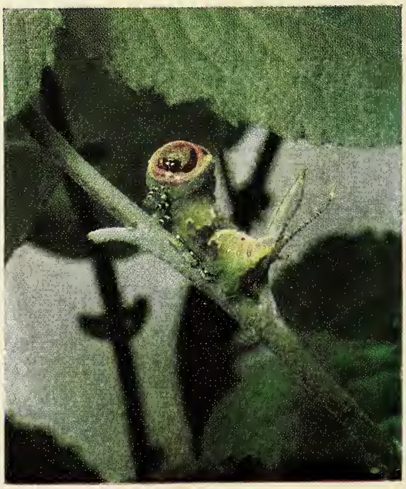
1. Garden Tiger, *Arctia caja*



2. Garden Tiger, in opened cocoon



3. Pale Tussock, *Dasychira pudibunda*



4. Puss Moth, *Cerura vinula*

Plate 22. WARNING COLOURS IN LARVAE

and 43), Satyridae, inhabits marshes and damp moorland from sea-level to over a thousand feet, the larva feeding upon grasses. It is an Ice Age relict, having a distribution in Britain from Staffordshire northwards. As might be expected, in the south of its range it inhabits only isolated localities which chance to suit it, and in many of these it has become extinct during the present century. However, from Cumberland northwards its distribution becomes fairly continuous and doubtless was more so before the changes brought by modern agriculture and the development of the Scottish lowland industrial zone. The insect exhibits a cline from north to south, the ground-colour becoming darker and the spots larger. On crossing specimens from North Cumberland with those from Northern Caithness in the extreme North-east of Scotland, intersexes appeared among the female but not among the male progeny. That is to say, isolation due largely to mere distance in what must until recent times have been a fairly continuous population, has been an effective barrier to the free flow of genes: so much so that the opposite ends of the cline are sub-speciating, as indicated by the appearance of sexual abnormalities in the heterogametic sex when specimens from them are crossed.

It is important to notice that clines for different characters may run in opposite directions; certain markings becoming progressively larger and others progressively smaller, for instance. Parallel clines, affecting several different species in the same way, are known in some areas.

Clines can be of different types, appropriately distinguished by a suffix. Thus a polymorph ratio-cline involves a gradual change in the frequency of polymorphic forms, or a passage from the monomorphic to the di- or polymorphic state. Such a situation is illustrated by several of the instances given in the chapter on polymorphism: for example, the Mottled Beauty, *Cleora repandata* L., Selidosemidae, and the dimorphism involved by its *conversaria* form in the South-west of England and the North-west of Scotland. Also the Burnet Moth, *Zygaena ephialtes* (page 51), provides an excellent example of polymorph ratio-clines in its European distribution.

Geographical Races in Isolation

Geographical races are often produced by cryptic resemblance to the rocks and soil in their respective habitats; in other instances no such association is detectable and they must be the outcome of the general adjustment of the organism to its environment. These two situations will be considered separately.

Probably the best examples of moths separated into races differing from one another in their cryptic colouring is provided by the two species to which reference has already been made in discussing protective devices (pages 96-7). The Annulet, *Gnophos obscurata* Schiff. (Plate 30), Selidosemidae, has an extensive range in the sea-board counties and some inland ones, the larva feeding upon rock-rose, salad-burnet and other plants. Its ground-colour is almost white on the chalk in Sussex (figure 12) and reddish-brown on the red sandstone of Devon (figure 13). The distribution of this species is by no means continuous, and I think these forms are geographically isolated from one another. The adjustment of this moth to dark peaty soil is equally striking, for specimens inhabiting areas of that kind are almost black. The example illustrated (figure 14) is from Oxshott, Surrey, where in this inland locality, a rather exceptional one for the species, the evolution of its colouring has certainly been perfected by isolation. It would be a matter of the greatest interest to study the, completely unknown, genetics of this moth. The colour-difference must be multifactorial or due to a gene, or perhaps to two or three major genes, with ‘ modifiers.’ We also require to know the degree to which the colour-types are isolated and the extent to which they intergrade.

Similar work is equally needed in the other species to which reference has just been made, the Tawny Shears, *Hadena lepida* Esp, (Plate 30), Caradrinidae. The necessary breeding work would probably be easier and the ecology more difficult, for this is a night-flying insect not easily found by day. It is not uncommon in England, where it is, generally of a light brownish shade, darker in the south-west (figure 10 from Cornwall). However, the population from the chalk of Kent and Sussex has modified its ground-colour almost to white (figure 9). It is probable that the two are connected by a short cline, but I am uncertain whether or not there is continuity between them. However, a black form *capsophila* (figure 11), has arisen in isolation on the dark rocks of the Isle of Man. Irish specimens vary from the typical colouring to dark grey according to the locality. Donovan is convinced that *capsophila* is a distinct species and that all the supposedly Irish *lepida* of whatever colour belong to it, as well as the Manx specimens: though he admits that the larva and pupa are indistinguishable from those of *lepida* and that the identification of the imagines is a difficult matter and the genitalia are identical, but he remarks ' the shape to me, at least, is different.' Abroad, the *capsophila* form, if it be distinct at all, is said to be more mountain-frequenting than is *lepida*. These discussions on whether or not local races should be judged distinct species are in fact rather unrewarding in the absence of genetic tests (pages 126 and 177). In any event, speciation is a gradual process, the amount of sexual isolation becoming progressively greater as we cross different forms, so that the point at which they are to be considered species is arbitrary.

Almost the only information on the cross-breeding of such races was obtained by Kettlewell, working on the Grass Eggar, *Lasiocampa trifolii* Schiff. (Plate 10), Lasiocampidae. He paired specimens from the light soil of Dungeness, Kent, which are of a pale putty colour (figure 5 male, 6 female), with dark reddish-brown forms from Cornwall (figure 4 male, 3 female). All the offspring resembled the Cornish parents, whose dark colouring may therefore have been inherited as a simple dominant, while the females among them were intersexual. Thus, whether the colouring is controlled by a simple genetic mechanism or not, these races have diverged sufficiently to build up subspecific differences in their sexual adjustments. It must not, of course, be supposed that a corresponding or greater degree of isolation would always have this effect; an instance in which it does not do so is described on pages 184-6. Whether or not the genetic adjustment of two races is such as to break down the sexual balance when crossed, depends upon the type of evolution that they have undergone.

We may now turn our attention to the other group of races produced in geographical isolation: that in which the differences involved do not depend upon the production of distinct types of cryptic coloration. This merits illustration from a somewhat wider range of instances.

The Northern Dart, *Amathes alpicola* Zett., from Shetland, from Aviemore in Inverness, and from Rannoch in Perthshire (Plate 27), has been described in discussing relict faunas; so have the two races of the Rannoch Sprawler, *Brachionycha nubeculosa* Esp. (Plate 28), from Inverness and from Perth. The Archer's Dart, *Agrotis vestigialis* Hufn., (all Caradrinidae), is a typical insect of sandy coasts though feeding mainly on bedstraw and grasses. It is whitish-brown in the male and grey-brown in the female. However, as already mentioned (page 132), a colony of it exists on the sandy hilltop of Cumnor Hirst, Berkshire, overlooking the Thames Valley at Oxford. Here the specimens are reddish-brown with less sharply defined markings than is usual. They must have evolved in isolation for a fairly long period.

The Beautiful Gothic, *Leucochlaena odites* Hb. (Plate 29), Caradrinidae, is a moth restricted to the coast, and especially to cliffs, from the Isle of Wight to Cornwall. The form shown in figure 4 is from Portland. At Babbacombe, South Devon, occurs a curious race, smaller, darker and differently marked (figure 3). At one time it was thought that this might be a distinct species. However, it has recently been more fully examined and the ordinary non-genetic tests, such as a study of the genitalia, give no indication that it is other than a local race of this moth.

The Purple-bordered Gold, *Sterrha muricata* Hufn., Sterrhidae, is a very local marsh-loving species found on wet heaths and moorland. In Britain it occurs principally in the New Forest, in Norfolk and in Westmorland, though existing also in other places, and the colonies are extremely isolated from one another. In the south of England the wings are yellow, bordered by small purple markings, while in the north the relative amounts of the two colours are reversed for there it has purple wings with a small central yellow dot. It is very local but abundant in Ireland. In Kerry, specimens ranging from predominantly yellow to predominantly purple occur together.

The distribution and forms of the Edinburgh Pug, *Eupithecia intricata* Zett., Hydriomenidae, are reminiscent of the Juniper Carpet (page 141). For this insect is restricted to junipers, and is found throughout Scotland wherever that plant occurs. It has also been taken, though sparingly, in the English Lake District and in Wales. It has, in addition, been able to adjust itself to the very different conditions provided by the junipers growing upon the Chilterns in Buckinghamshire, where it has developed the race *arceuthata* which is larger and paler than the typical form.

Numerous additional instances of this type of geographical variation are given in the chapter on relict faunas, and many more could be quoted. Only one of them, that of the Muslin Moth, *Cycnia mendica* Cl. (Plate 10), Arctiidae, has so far been studied genetically. It has been explained (page 163) that the normal form of this moth, *mendica*, is sexually dimorphic to a striking degree, the males being blackish (figure 7) and the females white with black dots (figure 8). This is the one occurring in Britain. The Irish specimens, on the other hand, belong to the distinct race *rustica* in which the males much resemble the females, being white, cream-coloured (figure 9), or occasionally ochreous. The difference between these two forms, which I have even heard described as sub-species, is due to a single gene without dominance. The heterozygous males are usually intermediates of a sandy colour (figure 10), but they are subject to a wide range of variation, which, of course, is greater in the F_2 than in the F_1 generation, the extremes being respectively as light as *rustica* and as dark as normal *mendica*.

We may with confidence predict that most of this variation is genetic, due to recombination taking place in the general gene-complex. Were the condition not sex-controlled, it would be an easy matter to select lines in opposite directions until *rustica* became dominant in the one and recessive in the other (page 214). However, the fact that the females are alike and relatively non-variable in the two races would make the work much more lengthy, for the potentialities for the production of *rustica* or *mendica* in the females used could not be ascertained by inspection.

The need for a re-interpretation of geographical variation in terms of genetics is clearly pressing. At present no distinction is made between those forms that are unifactorially, multifactorially, or wholly or in part environmentally controlled, or between those which have built up a slight or an extreme degree of sexual incompatibility on the way to speciation and those which have not done so. In discussing the part played by isolation and selection in producing races, sub-species and species, we are nearly always arguing in advance of ascertainable facts. Until those who study the classification of such forms on dead material turn to experimenting upon living specimens, they will not fully illuminate the subject; and it is to be hoped that this type of investigation will increasingly claim the attention of some of those already engaged upon genetic work.

Shetland Races

There is one group of local races that merits special attention: those occurring in Shetland. These are nearly all exceptionally dark forms, occasionally similar to those found elsewhere but usually unique. As Shetland has not been connected with the British mainland during the Holocene period, the non-migratory species there have evolved in isolation since the last glaciation. There was a land connection to these islands subsequent to its relatively severe second cold phase, for the long-tailed fieldmouse, *Apodemus fridariensis*, which inhabits them could not have survived this. Probably their present fauna dates from the early part of the interglacial phase which followed it, the second within the fourth main Pleistocene glaciation. It is worth while to describe and comment on a selection of these Shetland races.

The Marbled Coronet, *Hadena conspersa* Schiff., Caradrinidae, is a coastal species (page 133). Throughout the greater part of its range in Britain it has white fore-wings and smoky hind-wings. However, the white has an ochreous tint in some of the specimens from Cornwall and Devon; also in a considerable proportion of those from Wales, the Hebrides, Orkney and Shetland, where an increase in the dark markings also takes place. However, in Shetland this is usually a unicolorous blackish-grey insect, though it seems that more normal forms also occur there. The species is said to be widely distributed in Ireland, where the markings are rather darker but not more extensive than in England.

The variation of the Ingrailed Clay, *Diarsia festiva* Schiff., Caradrinidae, will be described on pp. 182-3, but in Shetland this moth has produced a small dark race, *thulei*, very unlike any other. The cline of the Autumnal Rustic, which has already been mentioned on page 172, may be regarded as an interrupted one, for the soft dove-grey of the English form gradually darkens through Scotland, while the sooty-brown race, *edda*, occurs in the West of Shetland.

One of the species that becomes dark in the Shetland Isles is the Red Carpet, *Xanthorhoe munitata* Hb., Hydriomenidae. This is illustrated on Plate 28, figure 9, which is the form *hethlandica*, with an ochreous ground-colour. Elsewhere, this insect has whitish-grey wings, (figure 8) and its distribution is that of one of the more widely-ranging Arctic-Alpines, being found in mountainous districts in Wales, Northern England, and in Scotland, where it is widespread in the north. It occurs also in Northern Ireland but is scarce there. Nothing approaching *hethlandica* appears to be known elsewhere in the British Isles. This is true also of the lead-coloured variety, *thules*, of the little Grass Rivulet, *Perizoma albulata*, Schiff., Hydriomenidae, which is similarly entirely restricted to Shetland. This insect, which is normally bone-coloured, becomes exceedingly variable there, some specimens actually being whitish. It has a wide distribution, occurring apparently wherever its larval food-plant grows; this is usually the Yellow Rattle, *Rhinanthus crista-galli*, a common semi-parasite upon grass-roots, but Dr. Cockayne informs me that the species feeds upon *Melampyrum* in Sutherland.

The distribution of the Grey Mountain Carpet, *Entephria caesiata* Schiff., has already been described in Chapter 11. Typically the fore-wings are grey, crossed with blackish lines, but both in Shetland and some of the Western Isles, Arran for example, this form is partially replaced by two others. One of them is approximately of the usual colouring but with a black central band, while the other is suffused with blackish all over. The Shetland specimens do not seem to be more extreme than those of the Western Isles.

Perhaps the most famous of the Shetland forms is that of the Ghost Moth, *Hepialus humuli* L. (Plate 28), Hepialidae. Elsewhere in Britain and Ireland, where the species is widespread and common, the males (figure 1) are immaculate, being china-white above with a glazed appearance, and sooty-brown below, while the females (figure 2) are light yellowish with indistinct ochreous markings. The Shetland population consists of the form *thulensis*(=*hethlandica*) in which the males are exceedingly variable. They range from specimens with the white rather dull-coloured, through those with ochreous marks, as normally found on the females, scattered over the white of the fore-wings, and smoky hind-wings (figures 4 and 5), to males with the white entirely replaced by yellow, and even to specimens considerably darker than normal females. The latter sex has a decidedly smoky tint in this form (figure 3).

The behaviour of this insect is remarkable. The males generally swing to and fro a few feet above the grass, making no progress but looking as if dangling on the end of a string. Their flight begins at dusk and they constantly vanish and reappear as the dark underside and white upperside are alternately exposed in the fading light by the movement of the wings. They are thus conspicuous objects and attract the attention of the females, which fly to them; a reversal of the process by which the sexes are usually brought together, in which the males take the active part. The Ghost Moth flies in late June. At this season in Shetland the night is never dark, so that selection no longer operates in favour of their conspicuous coloration; hence the breakdown which occurs there in the otherwise adaptive sexual dimorphism. It is interesting to notice that there appears to be no tendency to the production of *thulensis* in Orkney. With Mr. Malcolm Stewart of Hoy, I have caught and examined large numbers there, and all the specimens we have seen there might have been taken in the south of England. Indeed, so far as is known, the moths of Orkney either resemble those of the mainland or are distinct forms: they are not generally transitional to the Shetland races. This indeed is to be anticipated considering the more northern latitude and immensely greater isolation of Shetland, which is separated by 25 miles of exceedingly stormy sea from Orkney, while the latter group approach to within 6 miles of the Scottish mainland, the passage across the Pentland Firth being further reduced by the intermediate island of Stroma. Thus their isolation from Caithness is not very complete. I should stress, however, that, though so much more accessible, we have far less information on the entomology of Orkney than of Shetland, for collectors who have penetrated so far tend to go on to the latter group where rare species and unusual forms are known to exist.

One obvious question is posed by the Lepidoptera of Shetland. Why, if they differ at all, are they almost invariably darker than normal? The answer to it must be a tentative one. The general colour of the rocks, darkened still further as they are by the high humidity, and the peaty soil, all tend to produce a blackish background, to which the Shetland population has been able to adjust itself owing to its extreme isolation. These conditions recur, although often to a lesser degree, in many other islands, and dark insular forms are indeed widespread, though less marked where the isolation is not so extreme. At a time when some biologists attributed the occurrence of black moths in industrial areas to mutation due to salts of lead and manganese (Chapter 13), it was even suggested that the salt present upon the vegetation in coastal and insular localities gave rise to a somewhat similar effect. The impossibility of such a suggestion will be explained on page 197. Here it will suffice to point out that evolution is not controlled by mutation-pressure, that the view was put forward in singular indifference to the fact that the insects of chalk cliffs are far paler than normal (pages 174-5), as are those on light coastal soils in general (see the Grass Eggar from Dungeness, Plate 10), and that though most of the forms in the Western Isles of Scotland are indeed darker than usual, for reasons given, a few are, in fact, much lighter: thus an exceptionally white form of the Grass Rivulet is not uncommon in Lewis.

Types of Geographical Races

It has been pointed out that distinct races of the same species are sometimes continuous with one another because, having evolved in geographical isolation, the respective populations have subsequently extended their ranges and met; as, for example, those of an interglacial relict may do after an Ice Age. An example is provided by the Hooded Crow, *Corvus corone corone* L., and the Carrion Crow, *C. c. cornix* L. These are respectively the northern and southern forms of the same species, and they interbreed in a belt occupying Southern Scotland and North-western England, the hybrids being fertile. Another instance, discussed in *Butterflies*, pages 296-298, is supplied by the distinct Scottish and English forms of the Brown Argus butterfly, *Aricia agestis* Schiff.

It might have been supposed that two races would no longer have remained distinct when brought into contact and still able to produce offspring. Yet in these circumstances they often preserve their identity in spite of geographical fusion, which produces merely a belt of intermediate forms, showing that the separate populations are still fertile with one another in natural conditions. The zone of hybridisation may be extremely narrow, a mile or two across, or much wider: forty miles or so in the Brown Argus. Moreover, it is a region of high variability in which are found not only all mixtures between the characteristics of the two races but sometimes, as in the Brown Argus, individuals possessing features absent from both of them, owing to genic interaction.

This phenomenon is undoubtedly due to the fact that the two populations, having evolved independently, have each developed a gene-complex adjusted to their needs, a mixture between which will, almost by definition, be less well balanced than is either alone. Consequently, the hybrids even if freely produced will be at a relative disadvantage and therefore removed by selection, so preserving the pure forms intact in spite of their fusion. Recombination will ensure a high degree of variability where the different populations come into contact.

This situation does not seem to have been studied in British moths. Cockayne (1912-13) suggested its existence in the Bordered White, *Bupalus piniarius* L. (Plate 30), Selidosemidae, and there can be little doubt that he was correct. In the British Isles we have two forms of this species. One of them is the small Scandinavian race, in which the pale areas of the male are white (figure 5) and both the lighter and darker are as of the very distinct female are brownish (figure 6). It occurrs throughout Scotland and Northern England. The other inhabits the south of England. It is larger and has the pale area of the male ochreous (figure 7), while the female is throughout of an orange tint (figure 8). The two types meet and produce a variable hybrid population about the level of Shropshire and Cheshire, yet the zone of hybridisation is relatively narrow and, in spite of their fusion, the races remain distinct.

It seems likely that the Bordered White is an interglacial relict in the north and a Holocene invader in the south, and that the two have extended their ranges and met since the retreat of the ice. It is local and difficult to obtain, though widespread, in Ireland, where it approximates to the southern English form but is more variable. Presumably it reached that country during an interglacial phase when there was a land-connection to the South with Continental Europe (see Chapter 11).

This species is not difficult to rear or pair in captivity. Consequently, every effort should be made to study the genetics of so interesting an insect and to obtain adequate information on the extent of the overlap between the two forms and on its variability in that region.

In parts of Sutherland the northern race has given rise to the form *inversa*, perhaps common enough to constitute a dimorphism, in which the pale area of the females is white (figure 4), so that they have come superficially to resemble males in which the dark border is brown instead of black. The males which fly with them are of the ordinary northern type (figure 3). This variety may well be due to the action of a single gene sex-controlled to the female, but its genetics are unknown.

We may feel fairly confident that the races so far described are, wholly or in part, genetically determined. On the other hand, it is likely, but not certain, that the Ingrailed Clay, *Diarsia festiva* Schiff., Caradrinidae, provides an instance of geographical variation environmentally produced. This is one of those species already referred to on page 171 which are everywhere exceedingly variable. It is normally a woodland insect and as such is distributed throughout England and parts of southern Scotland and Ireland. However, a smaller form, *conflua*, having a similar range of variation to *festiva* itself, is to be found on moors and mountains. Its environmental nature is suggested but not proved, by the fact that it reappears wherever the insect colonises moorland country. However, the distinct Shetland race of this moth (page 178) has doubtless been evolved by selection acting upon genetic variation.

It has already been pointed out that some species remain similar, and apparently almost invariable, throughout the whole of an extensive though approximately continuous range (page 171). Certain moths are, however, subdivided into a number of isolated populations all of which are approximately the same. This situation could be illustrated from many examples. An excellent one is provided by an Arctic-Alpine, the Manchester Treble-bar, *Carsia sororiata* Hb., Hydriomenidae. This is purely an insect of the north, and it is subdivided into separate colonies depending upon the occurrence of its highly localised food-plants the Cowberry, *Vaccinium vitis-idaea*, and the Cranberry, *V. oxycoccos*. Yet the specimens comprising these different populations are in no ways distinct. Similarly the Streak, *Chesias legatella* Schiff., Hydriomenidae, is widespread in Britain and Northern Ireland but, feeding only upon Broom, *Cytisus scoparia*, it forms isolated communities; yet it is singularly uniform throughout its whole distribution. A further instance, drawn from a very different group, is provided by the Scarlet Tiger, *Panaxia dominula* L., Hypsidae. This has a wide range in Southern England (Map 10) but shows little sign of geographical variation, although existing in extremely isolated colonies in marshes and on river banks, where it feeds on comfrey. Perhaps the only instance of visible differentiation is provided by the famous population at Cothill, Berkshire (pages 210-13) where the specimens are decidedly smaller than usual and are polymorphic.

It must not be supposed that such apparent uniformity throughout a discontinuous distribution is other than superficial. The insects must be adjusted to their restricted environment in ways that are not reflected in their colour-pattern. For instance, the two extraordinary colonies of the Scarlet Tiger, one at the foot of the cliffs at Deal and the other on the sands at Pendeen (page 137), survive in conditions entirely abnormal for this marsh-loving species. They must be highly adapted to them, though the process has not affected their appearance.

It has been suggested by Beirne (1952) that the Small Yellow Wave, *Hydrelia flammeolaria* Hufn., Hydriomenidae, provides an instance of the independent evolution of distinct though apparently similar races. This moth feeds upon maple in the southern counties of England but upon alder in the northern ones and in Scotland. Beirne regards the latter race as an interglacial relict which had survived in western Scotland, and the maple-feeding population as derived from Holocene colonists. However, indigenous maple does not extend beyond the Midlands, and there seems no good reason why this insect should not merely have spread northwards in Holocene times, adapting itself to another food-plant beyond the range of the one which it normally prefers, as many others have done. Indeed several species change their food-plants from one part to another even of their British range. For example, Dr. Cockayne points out to me that specimens of the Yellow-ringed Carpet, *Entephria flavicinctata* Hb. (p. 157), from Yorkshire and Ireland are small and pale grey, while those from the Scottish Highlands are larger and very dark. The latter feed on the yellow-flowered *Saxifraga aizoides*, but the Yorkshire form feeds on a mossy saxifrage with white flowers (probably *S. hypnoides*). I do not know the food-plant of this moth in Ireland.

The Genetics of Geographical Races

A very large number of British moths have discontinuous distributions. In some of them distinct local races have been formed while in others they have not. Now if, as we all believe, geographical variation is an aspect of evolution, these differences or similarities have a genetic basis. Yet in hardly any instances is it known what, in terms of genetics, is meant by the statement that two races are ' different ' or are ' the same.'

It has already been pointed out that, though genetic theory can contribute so much to the study of geographical variation, precise information on the genetics of geographical races has so far been obtained in very few instances, one of them being the English and Irish forms of the Muslin Moth (pages 176-7). It seems essential also to discuss a related problem and inquire what genetic meaning can be attached to the statement that the same form of a moth occurs in localities that are isolated from one another. I know of only one piece of work which throws light upon that subject (Ford, 1953a).

The Lesser Yellow Underwing, *Triphaena comes* Hb., Caradrinidae, occurs throughout Britain and Ireland. Though somewhat variable, within most of this range it has ochreous brown fore-wings and yellow hind-wings with a black submarginal band (Plate 10, figure 1). However, in some parts of central and northern Scotland and in the Scottish islands it is a dimorphic species, for the dark phase *curtisii* (figure 2) occupies a considerable proportion of the population, perhaps up to fifty per cent or even more. This form is extremely variable. The fore-wings range from mahogany colour to black; the hind-wings are also suffused with black scales, in some specimens only slightly but in others so much as almost to obscure the yellow colouring.

It was found long ago *curtisii* is unifactorial and nearly but not quite dominant; that is to say, the heterozygotes are in general easily distinguishable from the recessives, the normal *comes*, but heterozygous and homozygous *curtisii* overlap one another. The darkest specimens seem always to be homozygotes and the lightest always to be heterozygotes, but the intermediates cannot be assigned to their correct genotype by inspection.

It is well known that this form occurs not only on the mainland of northern Scotland but also in the Hebrides and in Orkney. It is similar in appearance in these two groups of islands, yet Barra in the Outer Isles, whence the material was obtained for the investigation now described, is a hundred miles from the nearest point of Orkney; however, the Scottish mainland lies between them. Moreover, Barra is separated by fifteen miles of sea from the island of Skye, which is in effect part of the Scottish coast, being divided from it only by a river-like channel. Orkney is separated from the north coast of Scotland by the Pentland Firth, six miles wide at the narrowest point, near which is the small island of Stroma. It is clear, therefore, that the populations of this insect on Barra and in Orkney are very isolated from one another, and there is good evidence that the moth is not a regular migrant.

Specimens of *curtisii* were obtained from Barra and Orkney in order to compare their genetics. They were bred as separate lines for the three subsequent generations and it was found that this form was unifactorial and nearly dominant to *comes* in both of them. Moreover, by crossing homozygotes derived respectively from the two islands it was shown that the same gene was responsible for producing *curtisii*: for that form might of course have been the result of different genes with similar effects. When, however, heterozygotes of Barra and

Orkney origin were crossed, there was a complete breakdown in dominance among their offspring, which were distributed in an unclassifiable series from the blackest *curtisii* to ordinary *comes*; so that the two phases failed, for the first time, to fall into distinct groups.

We are now in a position to attach a more precise meaning to the systematist's statement that ' the same ' form of this species occurs in Barra and in Orkney. For in both places *curtisii* is not only visibly similar but is unifactorial, due to the same gene, and nearly dominant. Yet the means by which these apparently identical races have adjusted themselves to that gene are different, for its semi-dominance has been produced by a distinct set of ' modifiers ' in these two localities.

Such information is at present unique in the Lepidoptera, and very rare in the animal kingdom. Dobzhansky's analysis of chromosome-types in different races of the fly *Drosophila pseudo-obscura* may be compared with it (Dobzhansky, 1951). It is to be hoped that the genetic study of geographical races, whether similar or dissimilar in appearance, will be greatly extended in the near future, for such work will throw light upon the evolutionary processes which have produced them.

CHAPTER 13

MELANISM, INDUSTRIAL AND OTHERWISE

The Problem

THE INDUSTRIAL MELANISM of the Lepidoptera is the most striking example of evolution which has ever actually been witnessed in any living organism, animal or plant. Its importance therefore extends far beyond the confines of entomology, and since it is apparently more frequent here and in Germany than elsewhere, it provides a wonderful opportunity for moth-collectors in this country to contribute to biological knowledge; one lost to those whose interest is restricted to butterflies, for nothing of the kind has been observed in that group. It will be convenient first to give an account of the facts relating to this strange phenomenon and then to discuss its probable explanation.

During the last hundred years, black or dark forms of several species of moths have spread in manufacturing districts until in such places the normal specimens have been reduced to the status of rare varieties. These 'melanic' individuals were previously extremely scarce and have generally, though not always, remained so elsewhere in the country. In a few other instances they have in recent years succeeded in establishing themselves in certain, usually very restricted, rural areas, though they may or may not have become industrial melanics elsewhere in their range, in Germany for instance.

The Peppered Moth, *Biston betularia* L. (Plate XXIII), supplied the earliest instance of industrial melanism; its black variety *carbonaria* was first found in Manchester in 1850 and soon became common there. A similar change has since affected a number of other species, the better-known examples of which are listed in Table 1. This includes those which have become melanics anywhere within their range for, as will later be explained, the information on that occurrence in Continental Europe may throw light upon the existence of black forms in rural Britain. The list is, however, limited to moths whose distribution extends to these islands, though a few others which are not native here are also affected: *Aglia tau* L., for example.

An inspection of this table will show that the species in which melanic forms have recently spread are not all closely related but belong to several distinct groups. However, they all have one feature in common: they are insects in which at least a proportion of the imagines rest exposed, usually upon tree-trunks, rocks, walls or fences, and are protected by a cryptic resemblance to lichen, bark or wood.* This will be apparent from an examination of some of them which, together with their dark varieties, are illustrated on Plates XXIII, XXIV, 31. It will be noticed how well protected is the normal, speckled form of the Peppered Moth on light lichen-coloured bark, as shown on Plate XXIII. A few moths which hide out of sight in crevices or among dead leaves are, and always have been, black; for instance, the Black Rustic, *Aporophyla nigra* Haw., Caradrinidae. The fact that two-thirds of the species included in Table 1 belong to nearly allied genera of the Selidosemidae† is, I believe, due merely to the circumstance that these are on the whole widely distributed species which rest fully exposed concealed by their cryptic colouring, for some of the others are but distantly related to them.

An important aspect of these melanic forms is their genetics. The great majority of them are unifactorial and in every instance they are either partial or complete dominants; the latter is much the more usual condition, but in the Grey Arches, *Polia nebulosa*, the heterozygotes (known as *robsoni*, Plate XXIV, figure 4) are somewhat intermediate between the two homozygotes, which are respectively light grey (the normal, figure 3) and black with a white fringe (var. *thompsoni*, figure 5). Also in the Green-brindled Crescent, *Allophyes oxyacanthae*, the heterozygotes are not quite so dark as the homozygotes. Recessive melanics are well known as rare mutants, but in no instance have they spread either in industrial or rural areas. In a few instances, the dark forms are multifactorial, like those of the November Moth, *Oporinia dilutata*, but a gene having a more extreme effect than the others appears to be predominantly responsible for producing the

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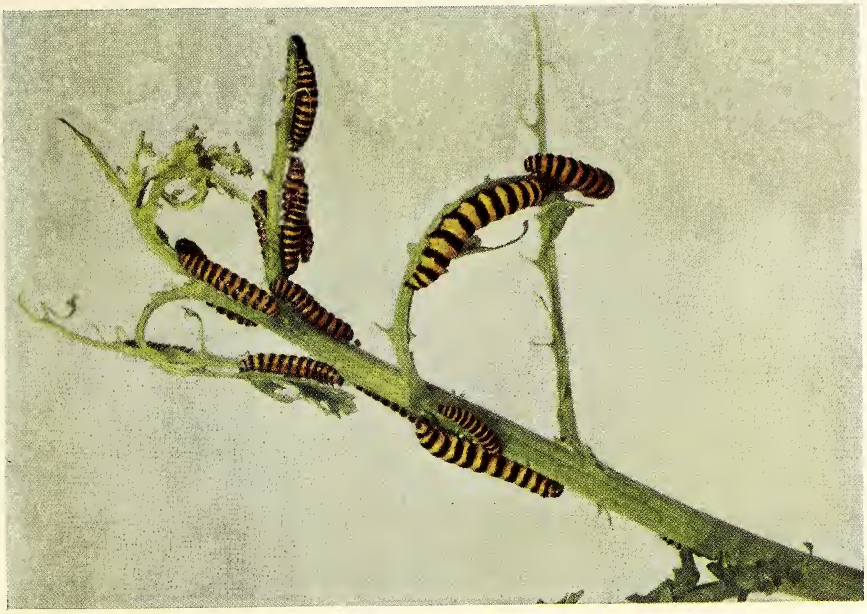
*The Continental species *Aglia tau* already mentioned is an exception to this statement, but only partly so, since it rests exposed upon low herbage.

†All the genera of this family which appear in Table 1 are closely related except *Gonodontis.*



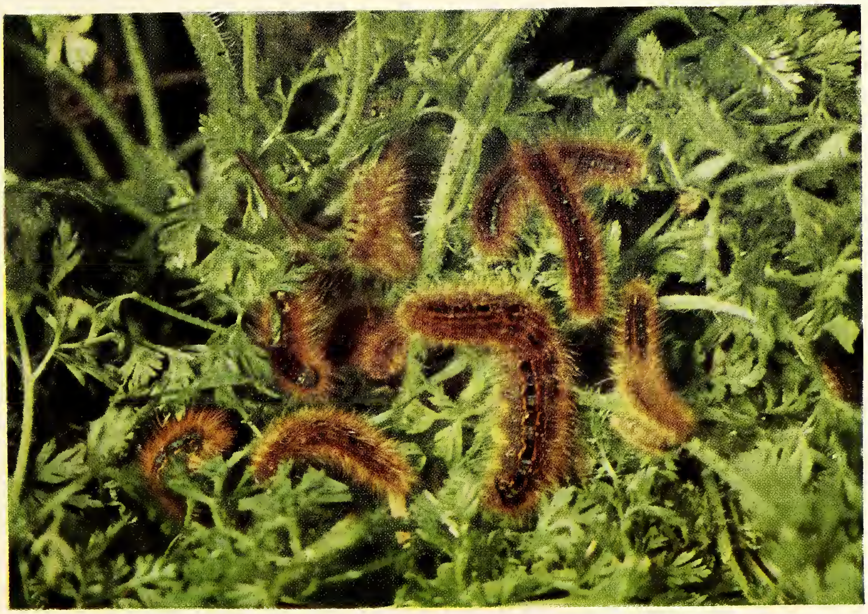
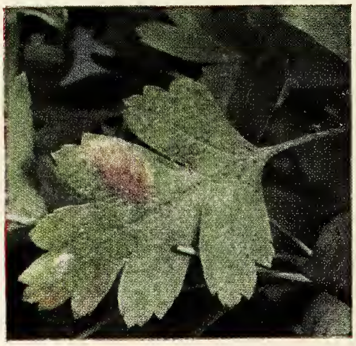
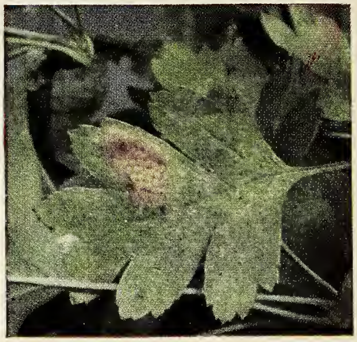


Plate 23. Warning Colours in Larvae

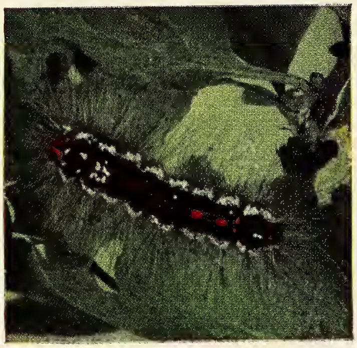
1. (*above*) Cinnabar, *Hypocrita jacobacae*. 2. (*below*) Ground Lackey, *Melacosoma castrensis*



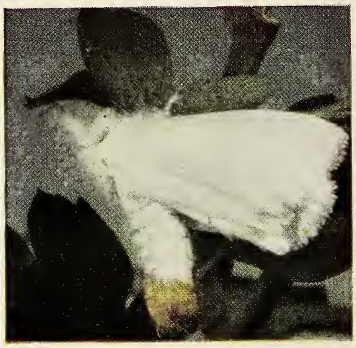
1. Gold-tail, *Euproctis chrysorrhoea*, eggs covered



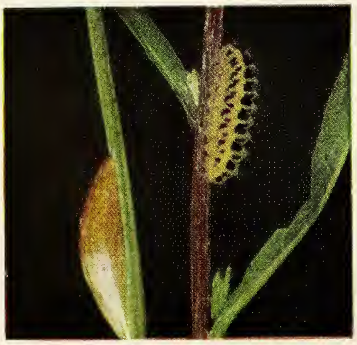
2. Gold-tail, eggs uncovered



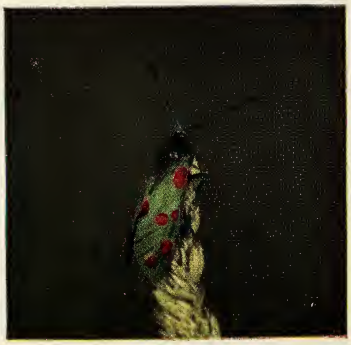
3. Gold-tail, larva



4. Gold-tail, imago



5. Six-spot Burnet, *Zygaena filipendulae*, larva



6. Six-spot Burnet, imago

Plate 24. THE GOLD-TAIL AND BURNET MOTHS
(Gold-tail, larva and imago, × $1\frac{1}{2}$)

black variety of this insect which has become common in the industrial north and in a few rural areas. As already explained, the melanism of the Black Arches, *Lymantria monacha*, is due to three genes, all dominants, which act cumulatively. All three are present in the darkest specimens. One of them, that with much the most considerable effect, is sex-linked and the other two are autosomal.* The melanic forms of this species have greatly increased in manufacturing regions in Germany but not in this country, though they have become not uncommon near Leighton Buzzard, and in Delamere Forest, Cheshire.

The Peppered Moth has two dark varieties. One of them is the well-known *carbonaria* (Plate XXIII), a complete dominant, which is of an intense uniform black except for a white spot on the base of the fore-wings. This is much the commoner of the two. The other, *insularia*, looks as if it were the heterozygote of *carbonaria*, for it is black with a scattering of white dots. However, it is controlled by a separate gene which is usually described as dominant, but I believe that the heterozygotes are slightly less extreme than the homozygotes. It cannot be detected when present simultaneously with *carbonaria*. So incomplete has been the genetic analysis of this species, though famous for its melanism, that it is even yet uncertain whether the *carbonaria* and *insularia* genes are multiple allelomorphs or are situated at separate loci, though such evidence as exists makes the latter alternative the more probable.

The Peppered Moth is generally common throughout England but ' normal ' (pale) specimens are now found only as rare varieties in the manufacturing districts of the north, so effective has been the spread of the *carbonaria* form in such places. It was there that it first established itself but, unlike many of the industrial melanics, it has spread outwards from them and now constitutes a considerable portion of the *betularia* population throughout most rural districts, so that to-day Devon and Cornwall, and perhaps Cumberland and Westmorland, are the only English counties where it is not known. The general history of the less common form *insularia* is similar, for it has become widespread also, but is certainly more often found in industrialised country; however, its frequency cannot be assessed by inspection where the insects are predominantly *carbonaria*.

The melanic forms of all the other species included in Table I

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*The different forms of *Aglia tau* are due to two multiple-allelomorphs, both semi-dominants (see pages 27 and 29).

Family	*Species*	*Country or District*	*Industrial or rural melanic*
CARADRINIDAE	Green-brindled Crescent *Allophyes oxyacanthae* L. (Plate 31, figures 10 & 11)	England	Industrial and rural
"	Grey Arches *Polia nebulosa* Hufn. (Plate XXIV, figures 3-5)	N. England	Industrial
LYMANTRIIDAE	Black Arches *Lymantria monacha* L. (Plate XIV, figures 1-6)	Germany England	Industrial Rural
HYDRIOMENIDAE	November Moth *Oporinia dilutata* Schiff. (Plate XIV, figures 7-10)	N. England	Industrial
SELIDOSEMIDAE	Brindled White-spot *Ectropis luridata* Bork.	England Germany	Rural Industrial
"	Small Engrailed *E. crepuscularia* Hb. (Plate XXIV, figs. 10 & 11)	England Germany	Rural and Industrial Industrial
"	Square Spot *E. crepuscularia* Hb.	England	Rural
"	Pale Oak Beauty *Boarmia punctinalis* Scop.	England Germany	Rural and indus'l Industrial
"	Satin Carpet *Cleora ribeata* Clerck	England	Rural
"	Mottled Beauty *C. repandata* L. (Plate XXIV, figures 6 & 7)	N. England Germany	Industrial and Rural Industrial
"	Willow Beauty *C. rhomboidaria* Schiff. (Plate XXIV, figures 8 & 9)	England Germany	Rural Industrial
"	Waved Umber *Hemerophila abruptaria* Thnbg.	London	Industrial
"	Pale Brindled Beauty *Phigalia pilosaria* Schiff. (Plate 31, figures 7-9)	N. England Germany	Industrial and Rural Industrial
"	Peppered Moth (2 forms) *Biston betularia* L. (Plate XXIII)	England	Both industrial; spreading to rural
"	Scalloped Hazel *Gonodontis bidentata* Clerck (Plate XXIV, figures 1 & 2)	N. England	Industrial
POLYPLOCIDAE	Poplar Lutestring *Tethea or* Schiff.	N. England Germany	Rural Industrial

TABLE 1: The spread of melanism in the Lepidoptera. (This incomplete list is restricted to species found in Britain).

are complete dominants unless otherwise stated. Most of those that have established themselves in rural areas have done so in quite restricted localities.

There are several melanic forms of the Brindled White-spot. The one which has become an industrial melanic in Germany is *cornelseni*. This is a simple dominant but I do not think it has been found in Britain, where the species does not enter industrial areas. Two melanic varieties, *fasciata* and *variegata*, occur in a few Kentish woods. Their genetics do not appear to be known but they may well be genetic or environmental phases of the same form.

The Square Spot has also become melanic in a few woods in Kent and, in addition, as Dr. Cockayne informs me, in a small wood in Gloucestershire. It does not enter industrial areas in Britain. The black form, *albigensis*, of the Poplar Lutestring, which has spread in so spectacular a fashion in industrial Germany (p. 205), seems in this country to have been found only in a restricted rural area in Yorkshire.

The Small Engrailed has a dark variety, *delamerensis*, which has spread in some manufacturing districts in England. It has also become common in Delamere Forest, Cheshire, and in some parts of Surrey.

The Pale Oak Beauty is an industrial melanic in Germany. The blackish *humperti* now occurs in the Birmingham area, while a dark grey form, *consobrinaria*, has spread in parts of Surrey, Kent and Sussex.

There is an intensely black variety, *nigra*, of the Satin Carpet which is now established, though not at a high frequency, in the yew woods extending from Mickleham to Box Hill. Furthermore, during the present century this moth has on the average become much darker throughout its range, but the genetics of the situation have not been worked out.

The Mottled Beauty has several dark forms. The true melanic, *nigra*, is, however, quite black. This has spread in a number of industrial areas, including the Liverpool and Sheffield districts.

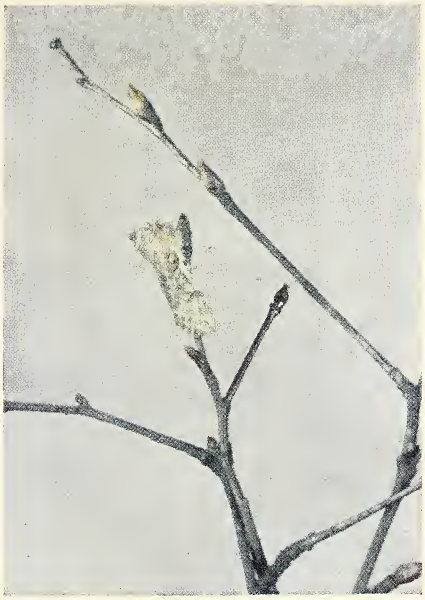
A black form of the Pale Brindled Beauty has become well established in some of the industrial districts of the north and round London and has spread thence into several rural areas. This is the simple dominant *monacharia* affecting both sexes. That due to a gene, sex-linked to the non-pairing region of the Y-chromosome (page 47) necessarily darkens the females only and, in this insect, these are wingless. I believe that it also has been found principally in manufacturing areas.

A number of other species have melanic forms the status of which is in doubt. They occur widely, sometimes increasing in frequency in the north, like those mentioned on page 172, and it is not clear that they are materially more common now than formerly. Moreover, their genetics have not been analysed. In these circumstances, it seems undesirable to include them in a discussion of the recent spread of melanism until more is known about them. Examples of such moths are: the Dark Arches, *Xylophasia monoglypha* Hufn., the Clouded-bordered Brindle, *X. crenata* Hufn., and the Marbled Minor, *Procus strigilis* Cl., all Caradrinidae.

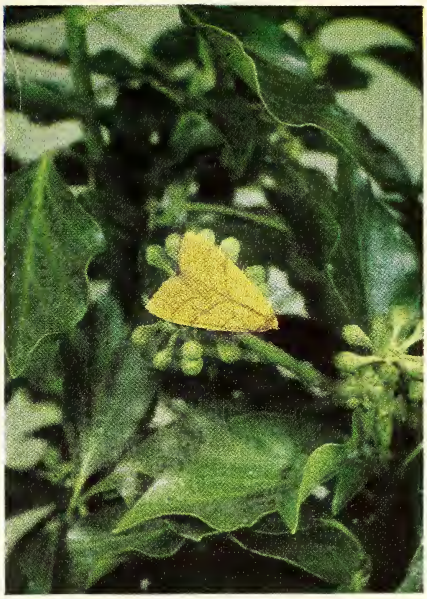
The status of the black variety *capucina* of the Green-brindled Crescent is very different from the others and difficult to assess; I have included it only tentatively as an example of the spread of melanism. The form seems to be unknown in Continental Europe. It is certainly widespread and frequent in some country districts in England; it occupies 10 to 20 per cent of the rural population in Oxfordshire. It is undoubtedly found also in manufacturing areas but whether it is relatively more abundant there I do not know. Moreover, unlike all the others listed in the table, I am uncertain whether it has become commoner in the last hundred years, though it has probably done so. Yet Edward Newman writing in 1869 speaks of it as 'of frequent occurrence,' and it was known to Haworth at the beginning of the last century, who named it the Dark Crescent. Its significance in the interpretation of industrial melanism will be discussed on page 202.

It will be noticed that Table 1 includes no instances of the spread of melanics in rural districts in Germany. Their absence is probably due to our lack of knowledge on the subject; indeed I have seen reports of this occurrence, but of a rather vague kind. Similarly, a number of other species could be included in the English list, but with less certainty than those here quoted; nor is information available on their genetics, and without it the subject cannot effectively be discussed. I should, however, be greatly surprised if any which have successfully established themselves prove to be recessives.

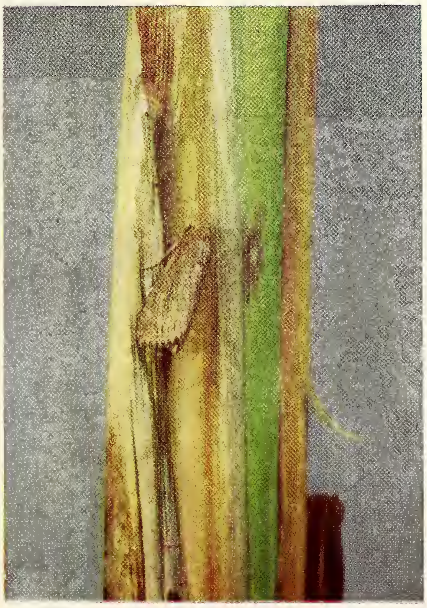
One additional aspect of the problem which deserves much attention but has received little is the occurrence and spread of melanic larvae. Harrison (1932) gives a good account of this in Northern England, listing the species in which it has been detected, the date of its first



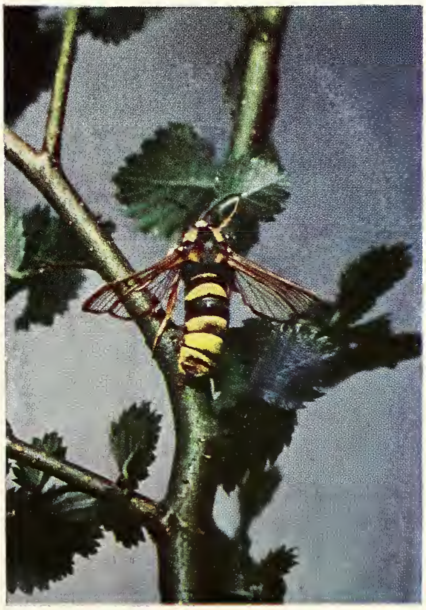
1. Yellow Horned, *Achlya flavicornis*



2. Orange Sallow, *Tiliacea citrago*



3. Bulrush Moth, *Nonagria typhae*



4. Hornet Moth, *Sesia apiformis*

Plate 25. CRYPTIC COLOURS AND MIMETIC COLOURING
(Yellow Horned and Bulrush Moth × $\frac{3}{4}$)

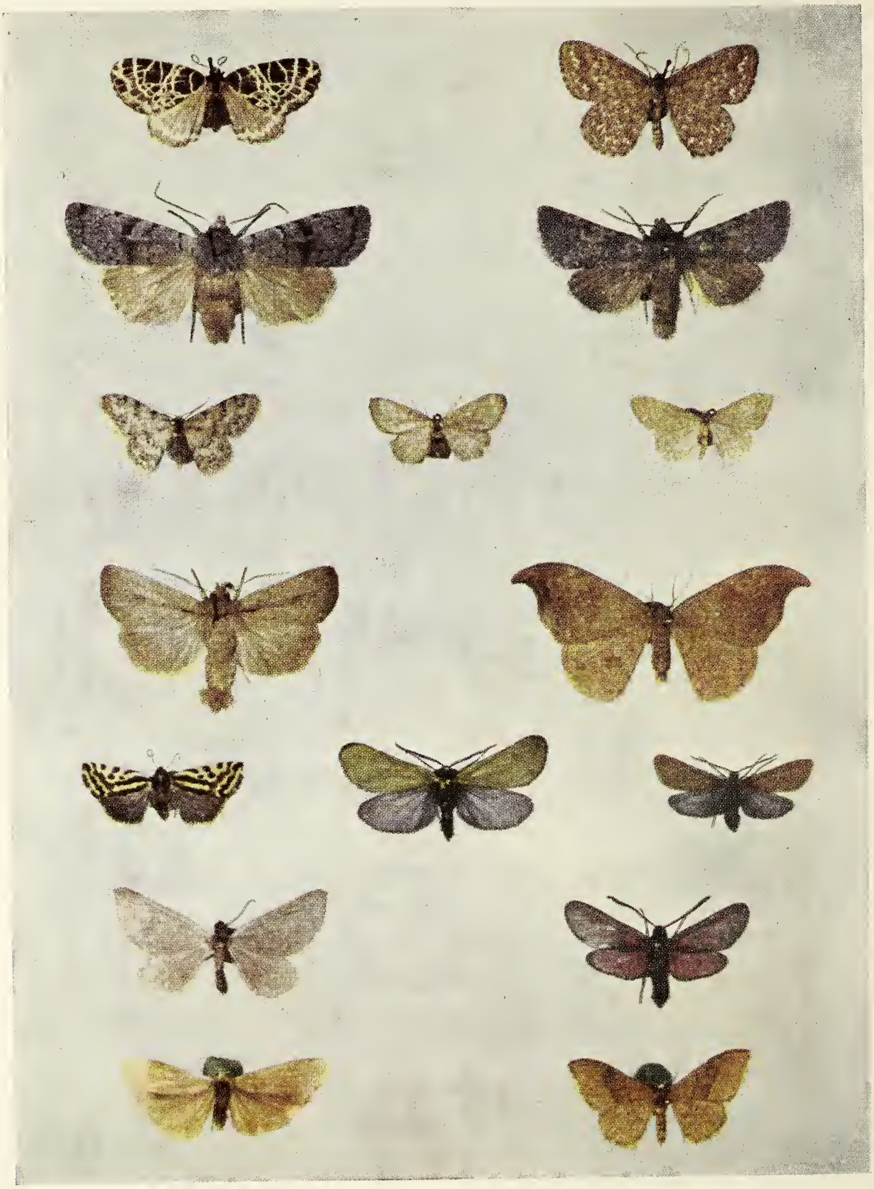


Plate 26

Plate 26. MOTHS WITH RESTRICTED DISTRIBUTIONS

1
WINDERMERE

2
LEWES
SUSSEX

3
PENMAENMAWR

4
ISLE OF MAN

5
N. WALES

6
ISLE OF WIGHT

7
BRISTOL

8
HORNING
NORFOLK

9
CLIFTON

10
LIVERMERE
W. SUFFOLK

11
Male
BRIGHTON

12
Female
BRIGHTON

13
W. SUFFOLK

14
NEW FOREST

15
DEAL
KENT

16
PORTLAND

---

1. Netted Carpet, *Eustroma reticulata;* 2. Lewes Wave, *Scopula immorata;* 3. Ashworth's Rustic, *Amathes ashworthii;* 4. The Grey, *Hadena caesia;* 5. Weaver's Wave, *Sterrha eburnata;* 6. Isle of White Wave, *Sterrha humiliata;* 7. Silky Wave, *Sterrha dilutaria;* 8. Fenn's Wainscot, *Arenostola brevilinea;* 9. Scare Hook-tip, *Drepana harpagula;* 10. Spotted Sulphur, *Emmelia trabealis;* 11 and 12. Scarce Forester, *Procris globulariae;* 13. Grey Carpet, *Lithostege griseata;* 14. New Forest Burnet, *Zygaena meliloti;* 15. Pigmy Footman, *Eilema pygmaeola;* 16. Portland Ribbon Wave, *Sterrha degeneraria*

appearance and status at the time when he wrote. The genetics of very few of these black larvae are known. They are simple dominants in the Green-brindled Crescent (Plate 31, figures 12 and 13), also in the Black Arches in which, however, they have not been found in this country, but are recessives in the Early Thorn, *Selenia bilunaria* Esp., Selidosemidae. Accordingly, as is to be expected (page 198), the condition has remained merely a rare variety in the last species. As already explained (page 26), the genes controlling larval and imaginal melanism work independently in the same species: the black moths have normal larvae and the black larvae give rise to normal moths (unless, of course, both genes happen to be present).

The study of the recent spread of melanic moths in manufacturing and rural areas is handicapped from an unexpected cause: a lack of knowledge on all aspects of the subject. One would have thought that this, the most outstanding instance of evolution in progress, would have proved a tempting field of ecological investigation in nature and experiment in the laboratory, but that is not so. Indeed, with a few exceptions, the information on it which exists is of a semi-anecdotal kind, generally acquired without the use of modern methods and techniques. More rigorous work is now in progress but it has not yet had time to advance far. It appears to me that one of the most important matters to be taken into account in explaining industrial melanism is the fact that the melanic varieties concerned are actually hardier than the normal specimens which, in ordinary circumstances, they have none the less failed to supplant. This is an extraordinary situation and it is obvious that it must be most exceptional. For it has been pointed out in *Butterflies* (page 276) that if an allelomorph enjoys even a one per cent advantage over its partner it will spread fairly rapidly, though not at a constant rate, through a population instead of remaining a rarity. Now, though such an advantage is considerable from an evolutionary point of view, it is too small to be detected even in carefully planned genetic work carried out on a large scale. That enjoyed by the black forms which have recently become common in nature must be far greater than this, probably of the order of ten to thirty per cent or more, since it has even attracted the attention of breeders who were not especially looking out for it. To take a specific instance, Haldane (1924) suggests that the gene-frequency of the *carbonaria* form of the Peppered Moth was 1 per cent, or less, in the Manchester area in 1848 and 99 per cent, or more, in

1898. This would require that the melanics have a 30 per cent advantage over the normally coloured specimens. Such differences in survival value of course manifest themselves in segregating families as departures from expectation in favour of the melanic insects.

A slight excess of this kind has indeed been reported more or less casually on a number of occasions in the course of ordinary breeding work, and it seemed desirable to establish its existence more decisively (Ford, 1940). The black variety of the Mottled Beauty, which has largely supplanted the more cryptically coloured specimens in certain industrial districts of the north, was chosen for this study. A slight but not significant excess of melanics over the expected equality was obtained when back-cross broods were reared in the usual way. It was then decided to make the conditions more rigorous, so as to increase the death-rate and put a premium upon any possible advantage which one form might have over the other. Accordingly, the work was repeated, but the larvae were now starved on alternate days. As a result of this treatment, fewer of them survived to produce moths. Among these, however, the black specimens were found to be markedly the commoner, and to an extent which was statistically significant. For example, in one set of experiments the numbers were as follows: a total of three families supplied with abundant food gave 101 melanics and 91 normals (96 of each form expected); while five starved families produced 51 melanics and 31 normals (41.5 of each expected).* It should be remembered, however, that in natural conditions every pair of moths produces on the average but one pair only, so that the elimination must ordinarily be far greater than in these tests. Consequently, though some of it may not be selective from this particular point of view, the relative advantage of the black specimens must be greater also.

Corresponding work on additional species is badly needed. So far it has been extended only to the Scalloped Hazel, when similar results were obtained, but collectors who have bred several of the others have remarked on the superior hardiness of their melanics also. That is to say, the gene responsible for producing an excess of black pigment must in addition influence the general physiology of the insect in a way favourable to its survival. This, however, does not mean that the type of metabolism associated with a heavy production of melanin is in itself advantageous, for recessive melanics are much more delicate than the normals, though they are often as dark as the blackest of the dominant type. Several examples of recessive melanism are illustrated on Plate 31: the Early Thorn, *Selenia bilunaria* Esp. (figures 1 and 2); the August Thorn, *Ennomos quercinaria* Hufn. (figures 3 and 4); and the Engrailed, *Ectropis bistortata* Goeze (figures 5 and 6). It seems that a less dark form of the latter species is a simple dominant, and this might well become an industrial melanic if the appropriate situation arose.

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* Here $\chi^2_{(1)} = 5.8$, for which $P < .02$ (that is to say, a 1 in 50 chance).

The Explanation

Several theories have been advanced to explain this spectacular increase in melanism during the last century. The claims of each of them must therefore briefly be considered. First, there is the obvious one dependent solely upon simple cryptic colouring. Tree trunks, and vegetation generally, are blackened by soot in many manufacturing districts, and here the dark forms may be the less conspicuous. That they sometimes are so, and that on the contrary they must be eliminated in ordinary circumstances, can hardly be in doubt in view of Mr. Beaufoy's beautiful photograph of normal and melanic specimens of the Peppered Moth resting on both light and dark bark, shown on Plate XXIII. I vividly remember the first occasion on which I found the *carbonaria* form of this insect in rural conditions. Walking through an oak wood in a country district in Oxfordshire, I noticed what appeared to be a large lump of soot about eight feet up the trunk of a tree twenty yards or more away. I need hardly say that it would have been impossible to see a cryptically coloured specimen in these circumstances at half that distance. The shift of advantage from one to another of these forms in industrial and unpolluted country respectively cannot be denied; but when taken alone as an explanation of the phenomena now under review it fails at the outset, for it does not even cover the facts. Manifestly it offers no solution of the spread of melanism in rural areas; indeed judged on its face value it only makes that occurrence the more mysterious: nor does it throw any light upon the extraordinary physiological difference between the pale and dark forms to which attention has been drawn. Evidently it must be a contributing factor only to a situation of greater complexity.

Secondly, it has been claimed by Harrison that the increase of melanism in manufacturing districts is due to the chemical induction of mutation. He found that the soot coating the leaves and bark in such areas contains salts of lead and manganese and suggested that these substances, when eaten by the larvae, caused the mutation of genes responsible for an excessive formation of the black pigment melanin. The difficulties of such a view are insuperable. Obviously it is subject to the identical double criticism just levelled at that based upon simple cryptic colouring. But there are other objections to it at least as weighty. Thus those who have supported it do not appear to have considered the mutation-rate involved, which would have to be much greater than the maximum so far produced even by the use of penetrating radiation. Indeed the objections to all theories of evolution which are supposed to work by controlling mutation are extremely cogent (see Ford, 1948, Chapter 3). Furthermore, such concept throws no light upon the curious dominance relationship to which attention has already been directed (page 188): that is to say, only genes dominant or semi-dominant in effect have taken part in the recent spread of melanism.

Harrison has several times attempted to demonstrate experimentally the production of melanic varieties by mutation due to salts of lead and manganese. His results are subject to criticism on several distinct grounds. First, they have been repeated by two independent workers, who failed to confirm them though they used larger numbers than he. Secondly, he worked principally upon the Early Thorn (Plate 31, figures 1 and 2), in which the melanism he studied is recessive. This was a most unfortunate choice of material, for it required the use of extremely rigorous controls to make sure that the gene concerned was not introduced in the heterozygous state: controls which R. A. Fisher has shown to be inadequate. Had a species in which the dark form is dominant been employed, no such difficulty would have arisen. Thirdly, Harrison was thereby investigating a phenomenon which seems never to have occurred: the spread of recessive melanism. Thus his interpretation, which caused considerable controversy in past years, need no longer be considered.

I have long maintained that the success in recent times of melanic varieties of moths is to be explained only upon lines which take into account all the phenomena associated with it. The view which I put forward can now briefly be summarised.

It is suggested that all those genes which confer any physiological advantage upon the individual must have spread through the population unless handicapped by some counter-balancing disadvantage, such as the destruction by excessive melanin formation of the cryptic colour-pattern upon which the safety of the insect depends. Genes have multiple effects of varying kinds and some of those responsible for blackening the insect increase, and others decrease, its resistance to adverse conditions. It seems hardly possible that the melanics whose stamina is reduced could ever spread, for in normal circumstances they would be handicapped both physiologically and ecologically. They must, in fact, have consistently been at such a disadvantage as to have evolved into recessives (*Butterflies*, pp. 257-62). However, in those in which superior hardiness competes with the obliteration of their colour-pattern, advantage and disadvantage may have been too nearly balanced for recessiveness to have arisen. On the other hand, when the wings are flooded by black pigment, the effect of dominance may be produced even though it has not been achieved by selection; for if one dose of melanin reaches visual saturation the effect of doubling it will not be apparent. All that we can say about such forms is that they have not been sufficiently handicapped to have become recessive. However, in the man-made environment of industrial areas, the balance of nature may be so subverted that it becomes possible for species to make use of physiological advantages which they could not previously exploit on account of the melanism to which the genes concerned also give rise. In such circumstances ‘ dominant,’ or rather ‘ non-recessive,’ melanics may be able to spread; recessive melanics, on the other hand, could not do so for, being physiologically inferior, they remain useless.

The success of non-recessive melanism in industrial areas is probably due to three main causes. First, as shown on Plate XXIII, melanic specimens, normally so conspicuous, may actually be the better concealed in the blackened countryside of manufacturing districts. It is, of course, not necessary that their colour should actually become an asset (as in the Peppered Moth it seems to be), but merely that its disadvantage should be reduced until outweighed by the value of their physiological superiority. Secondly, owing to the general destruction of life in such places, predators (pp. 203-4) will be fewer and therefore the importance of concealing coloration relatively less. Thirdly, a gene which in normal circumstances is only at a slight physiological advantage may be at a considerable premium in the unsatisfactory conditions of the soot-begrimed countryside, where quite probably the death-rate of the larvae is unduly high owing to their contaminated food: a conjecture which receives strong support from the laboratory experiments already mentioned, in which the relative superiority of the melanics increased as the conditions deteriorated.

In addition, H. B. D. Kettlewell has drawn attention to the importance of the Aphis secretion known as honeydew in increasing the amount of such pollution upon the leaves of certain trees and bushes; notably elm, lime, oak and hawthorn. This substance accumulates during the summer, particularly in dry periods, and being sticky collects dirt of all kinds, so that in towns and industrial districts the foliage affected by it may be almost black. Consequently, its presence adds greatly to the amount of impurities, often containing injurious chemicals, consumed by certain larvae in such regions.

The establishment of melanism in restricted colonies of certain moths in rural England evidently constitutes a related but somewhat different problem. The key to it is undoubtedly supplied by the fact that here the greater part of the countryside is a product of civilisation far removed from its primeval state. One might expect, therefore, occasionally to find places in which the ecological balance of some species has been so upset as to favour increased viability relatively more than cryptic colouring. It is precisely those forms in which the advantage of superior hardiness is just held in check by the obliteration of concealing patterns which are capable of exploiting such a situation. How long they have done so does not seem to be known. Changes in forest management in the last hundred years are probably quite capable of precipitating such an event which, in some instances, may be very recent; just as the homostyled form of the Primrose is at the present time displacing the normal heterostyled one in an extensive tract of " unspoiled " countryside in Somerset. Such human interference may be direct, through selective felling and new methods of silviculture, or indirect, depending upon its influence on wild life in general and especially in reducing the numbers of the predators which destroy these moths. It is likely, however, that in discovering the unsuspected extent to which leaves in rural districts are polluted by soot, especially those affected by honey-dew, Kettlewell has found the most potent cause of non-industrial melanism. He has demonstrated that a surprising amount of such contamination is present on the vegetation in apparently unspoiled country. This is the result of drifting smoke

Plate 27. NORTHERN AND MOUNTAIN MOTHS

1
Male
SHETLAND

2
Female
SHETLAND

3
Male
AVIEMORE

4
Female
AVIEMORE

5
Male
RANNOCH

6
Female
RANNOCH

7
fully grown larva
AVIEMORE

8
BRAEMAR

9
OBAN

10
Male
INVERNESS

11
fully grown larva
RANNOCH

12
Female
INVERNESS

13
Male
RANNOCH

14
Female
RANNOCH

15
ROSS-SHIRE

16
RANNOCH

1-7. Northern Dart, *Amathes alpicola;* 8. Mountain Burnet, *Zygaena exulans;* 9. Oban Burnet, *Zygaena achilleae;* 10-12. Black Mountain Moth, *Psodos coracina;* 13 and 14. Netted Mountain Moth, *Isturgia carbonaria;* 15. Small Dark Yellow Underwing, *Anarta cordigera;* 16. Broad-bordered White Underwing, *Anarta melanopa*

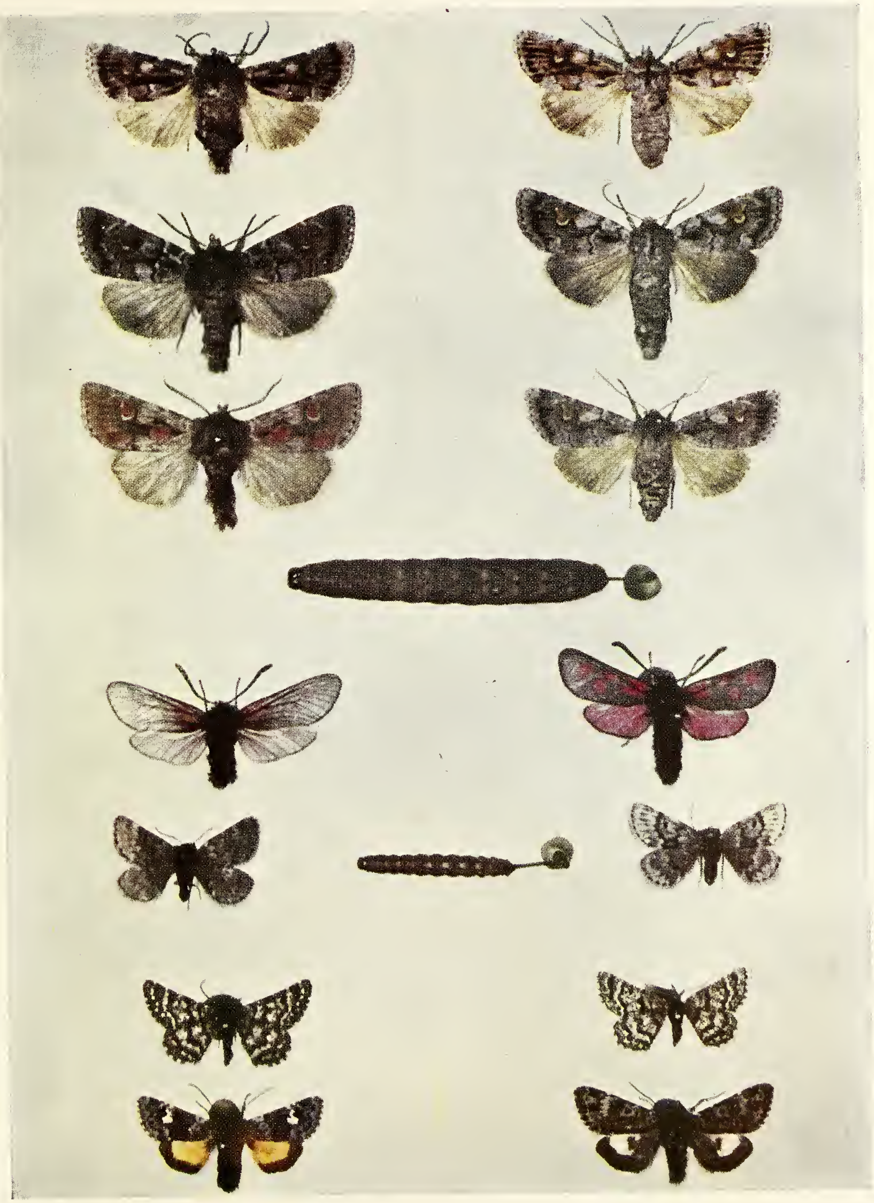


Plate 27

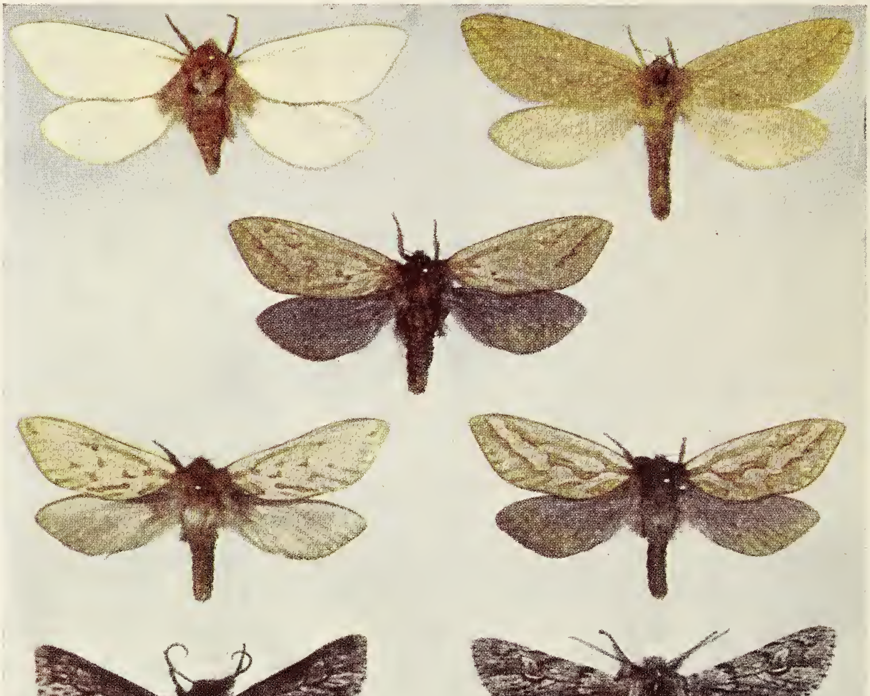


Plate 28

1
Male
RUGBY

2
Female
CAMBRIDGE

3
Female
SHETLAND

4
Male
SHETLAND

5
Male
SHETLAND

6
RANNOCH

7
AVIEMORE

8
SUTHERLAND

9
SHETLAND

10
BUCKINGHAMSHIRE

11
SHETLAND

1-5. Ghost Moth, *Hepialus humuli;* 1 and 2 typical, 3-5 *hethlandica;* 6 and 7. Rannoch Sprawler, *Brachionycha nubeculosa;* 8 and 9. Red Carpet, *Xanthorhoe munitata;* 10 and 11. Juniper Carpet, *Thera juniperata* from towns, and probably from railways, while the pall of soot-laden fog which spreads from London far across Surrey and Kent, and widely from manufacturing areas in the north, is a phenomenon the existence of which is now well recognised, though its biological effects have not been appreciated. Its importance in favouring the physiologically hardier melanics may well be decisive in ensuring their spread.

It will be noticed that the dark forms which have established themselves here and there in unpolluted country in England have the very qualifications which should enable them to become industrial melanics. That several of them, such as the Brindled White-spot and the Pale Oak Beauty, have actually done so in Germany, is due merely to the fact that there the range of these species includes manufacturing districts but does not do so here, or perhaps they were eliminated from them in England before the mutation producing melanism had had time to take place. It is curious that the Willow Beauty, which is found in smoke-begrimed areas in this country, does not seem to have become an industrial melanic here though, as pointed out to me by Dr. E. A. Cockayne, the melanic variety has occurred at Norwich. That it has done so in Germany shows it to be potentially capable of such evolution, which may well take place in England in the future. Perhaps the black variety has not yet occurred sufficiently often in appropriate conditions in Britain to be picked upon by selection.

Since modern conditions sometimes allow the spread of black forms in rural England, one would not expect that process always to be confined to restricted localities but occasionally to affect a species in one but not another extensive tract of its distribution. That situation is realised in the Green-brindled Crescent, in which the melanic form is common in some country habitats in England but is apparently unknown in Continental Europe.

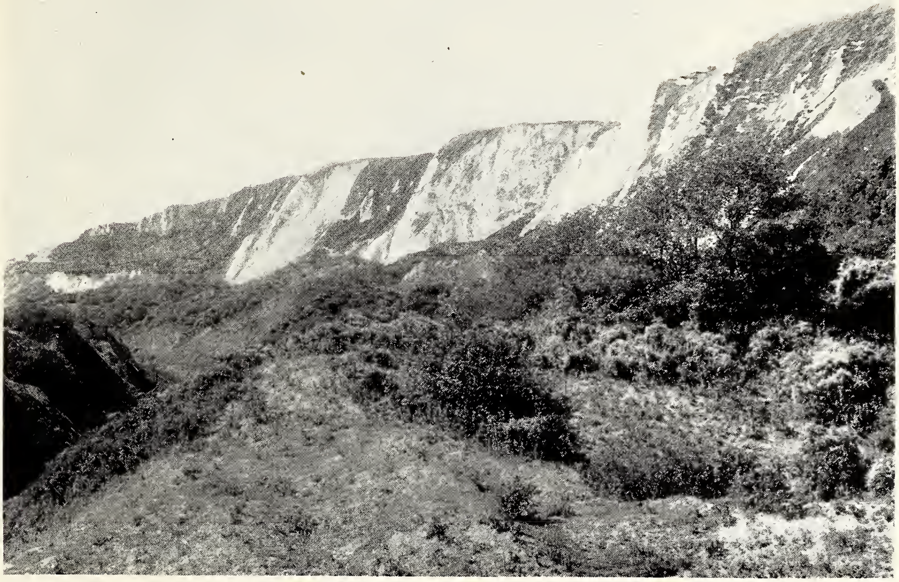
A manufacturing district in which a moth has become melanic is naturally surrounded by a region where the black form declines to the status of a rare variety. The extent of this penumbra is of course variable, depending upon the ecological requirements of each species; also upon the local conditions, for the intergrading zone between polluted and unpolluted country may be wide or narrow. However, several melanics have spread far beyond the industrial areas where they first established themselves, but none has been so successful in this as the two black forms of the Peppered Moth, which are now frequent throughout the majority of the English counties. It seems that they have been able rather widely to exploit the changes which have transformed our land so far from its primeval state, but instead of having to spread from rare mutants at an extremely low density they have suddenly acquired a numerically vast reserve from which to invade the woodlands and hedges of rural England. This may well have had an additional consequence. It has probably given the species a chance to evolve rapidly and improve its physiological advantages owing to the great opportunities provided for the operation of selection. We have indeed some evidence that the effects of the genes giving rise to the black Peppered Moths, which have so successfully set out from the industrial districts of England to establish themselves in rural areas, are not identical with those they produced a hundred years ago. For Dr. Kettlewell, after examining early examples of *carbonaria* from old collections, finds that its dominance has increased during that period and its other characters may equally well have been adjusted also. It is not clear, in fact, that the black Peppered Moths captured during the third quarter of last century could have spread as effectively through rural Britain as their descendants are doing to-day.

It had always appeared that birds are the only predators which could selectively eliminate melanic Lepidoptera in unpolluted country, and the pale cryptically coloured specimens in manufacturing districts. For, to be effective from this view-point, the moths must be destroyed in relation to their background when at rest. Those killed by bats will be caught upon the wing; and so will the majority of those secured by predacious insects, though they are not likely to be many. Moreover, we may fairly presume that the colour of a moth does not affect the chance that it may be entangled in a spider's web. Curiously enough, it is an almost unrecorded event for a bird to pick a moth off a tree-trunk, and consequently many entomologists have doubted its occurrence, save in quite exceptional circumstances. Yet were such selective elimination, and on a large scale, not a reality, the explanation of industrial melanism here advanced would be untenable. Indeed, the fact that it takes place with great frequency was only established by the work of H. B. D. Kettlewell in 1953, and it then became clear why the destruction of moths in this way had not previously been detected.

In the early summer of that year Kettlewell, working in the experimental aviaries at Cambridge, found that normal and black Peppered Moths were selectively eliminated by Great Titmice, *Parus major*. This was sufficiently promising to warrant an extensive investigation in the field. With the kind permission of the owner, he therefore liberated 171 normal Peppered Moths, *betularia*, and 416 of the black form, *carbonaria*, in the Cadbury Bird Reserve, which is affected by smoke-pollution from Birmingham. At that time, the titmice, Paridae, normally perhaps the most serious predators, were otherwise engaged, feeding at the tree-tops on the moth *Tortrix viridana*. Having noted the positions of the Peppered Moths which he had released upon the tree-trunks, Kettlewell watched them from a distance with glasses and saw them destroyed in large numbers by Robins, *Erithacus rubecula*, and Hedge-Sparrows, *Prunella modularis*. The act of taking each insect was accomplished with extraordinary rapidity, almost in a flash, and could never have been detected without intensive large-scale work of this kind.

Moreover, Kettlewell had identified each of his specimens with a dot of cellulose paint, but on the underside so that the marks could not be seen by birds, for this moth rests with outspread wings (Plate XXIII). By the use of mercury-vapour light-traps, Kettlewell was able to recover his marked insects at night, and had the satisfaction of detecting the better survival of *carbonaria* in this area. Out of a total of 584 males released, he recaptured 141 in this way (the females fly but little and therefore rarely visit a light). These recaptures consisted of 27.5 per cent of the black moths which had been liberated and 13.0 per cent of the pale ones. Though much more work of a similar kind remains to be done, the mystery surrounding the selective elimination of normal and melanic Lepidoptera has thus been solved.

The history of industrial melanism is a chronicle of lost opportunities. For once a striking evolutionary change has taken place so rapidly and extensively that the process could be analysed in detail. Collectors in many parts of the country could for a hundred years have obtained precise information on the rate at which the black forms spread and the conditions in which they do so. In this they have constantly failed, and our ignorance of the subject remains profound. We know that in certain places melanic specimens have, within living memory, almost completely replaced those with cryptic colouring and, with very few exceptions, that is all. Indeed, one of the most accurate observations is that of Gerschler who reported that the black variety



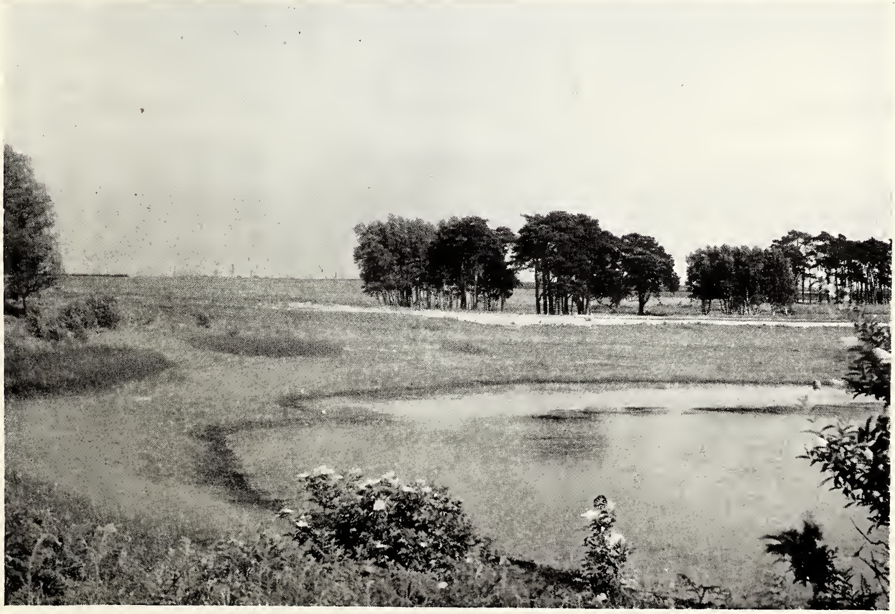


Plate XXI. 1 (*above*). The Warren, Folkestone; 2 (*below*). The Breck District

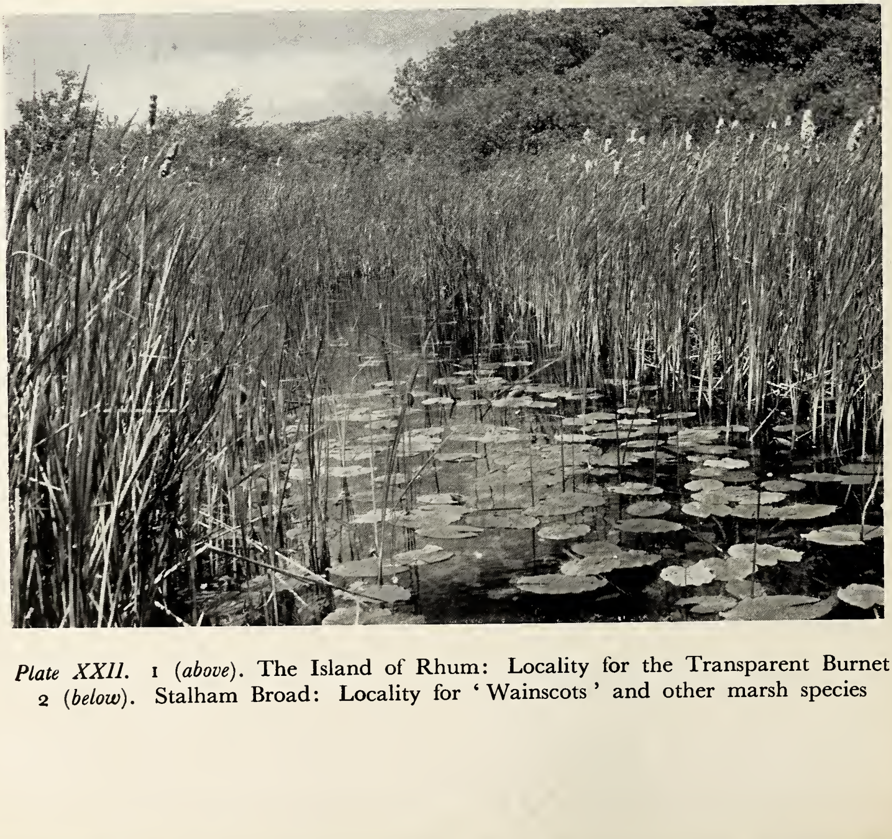


Plate XXII. 1 (*above*). The Island of Rhum: Locality for the Transparent Burnet
2 (*below*). Stalham Broad: Locality for 'Wainscots' and other marsh species

of the Poplar Lutestring was 'very rare' in the neighbourhood of Hamburg in 1904 and that in 1911-12 he collected large numbers of larvae there and found that ninety to ninety-five per cent of them gave melanic imagines. Indefinite as is this statement, it strongly suggests the magnitude of the change in progress, for this species has but one generation in the year. A detailed investigation of it over this period, using adequate sampling methods and giving accurate statistics, would have become a classic in the study of evolutionary genetics; and the facilities for such work, on other species, have been still better in England. Even the available vague statements of the spread of the *carbonaria* form of the Peppered Moth in the Manchester district have enabled Haldane to make an approximate estimate of its advantage over the normally coloured specimens (pages 194-5).

Investigations of this type are at last being undertaken; but methods for reducing pollution from factories are being improved while the laws for enforcing them are more strictly applied, so the work may not be quite so easy in the future as it would have been in the past. One promising aspect of it now in hand is the experimental approach of founding artificial colonies in which the proportion of melanic and non-melanic forms are known at the start and then determined throughout subsequent generations. These are being established both in rural and industrial areas, and their fate should throw fresh light upon the subject.

The record of genetic studies on industrial melanics has been more encouraging than that of the field-work, but the status of a number of imaginal forms and of nearly all the larval ones is still unknown. Also, we are ignorant of the relationship between the different genes for melanism which occur in the same species, and in every instance much more information is required on the relative hardiness of the three genotypes in varying conditions, genetic and environmental.

All these points require careful study before the details of industrial melanism can be filled in, though its general outline seems now to be indicated. Finally, it should be noticed that this is an instance of transient polymorphism* (page 64), the most striking ever encountered, in which distinct forms have spread through certain populations as the result of selection. To take a specific instance, a hundred years ago the *carbonaria* phase of the Peppered Moth was a rarity in the neighbourhood of Manchester; it increased until the insect became dimorphic in that district, but instead of remaining in that condition balanced by contending advantages and disadvantages as in a permanent polymorphism, it continued to spread there until the ‘ normal ’ cryptically coloured form was itself reduced to the status of a rare variety. Such a process, taking place repeatedly in this country now and in the past, is a challenge to moth collectors to contribute to biological knowledge in a field which provides them with unrivalled opportunities for doing so.

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*It is possible that instances may be found in which the heterozygous melanics are at a physiological advantage and the homozygous ones at a disadvantage compared with the pale homozygotes. This would produce balanced polymorphism.

CHAPTER 14

EVOLUTION

Population Studies

Julian Huxley has pointed out that, owing to the title of the greatest of Darwin's books, the importance of the origin of species has been somewhat over-emphasised in discussions on evolution. Other fundamental aspects of the subject include the adjustment of the organism to the effects of individual genes, whether advantageous or disadvantageous, its adaptation to the environment, in the widest sense of that term, and the formation of geographical and other races and of clines. These are all examples of what has been called micro-evolution, for they modify rather than transform species. Moreover, the changes involved may take place rapidly enough to fall within the scope of human observation and experiment. On the other hand, the origin of species and of higher taxonomic groups, and the establishment and maintenance of long-range evolutionary trends, are usually lengthy processes regarded as constituting macro-evolution. However, these terms cover differences of degree not of kind. Thus I do not doubt that new species could be produced by selective breeding in the laboratory and, in plants at least, they occasionally arise at a single step:* indeed both speciation and extinction are subjects which could well be included under either heading. Some of these problems have been discussed in *Butterflies*, and a few others only will be considered here.

Evolution remains a highly controversial phenomenon, but it is now being illuminated by experiment; a technique in accord with Darwin's own methods rather than those of his contemporaries or his successors in the generation immediately following him. That it has found favour to-day is due primarily to the rise of genetics: the most fundamental branch of biology and the one whose influence, extending

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*This may occur in allopolyploidy, when a doubling in the number of chromosomes gives fertility to a previously sterile hybrid.

1
FRESHWATER
ISLE OF WIGHT

2
ISLES OF SCILLY

3
S. DEVON

4
PORTLAND

5
OXFORD DISTRICT

6
DORSET

7
'ENGLAND'

8
ORTON
CUMBERLAND

9
DEVON

10
'ENGLAND'

11
ABERDEEN

12
N. STAFFORDSHIRE

13
IPSWICH

14
UNDERSIDE
IPSWICH

15
ACHANALT
ROSS-SHIRE

---

1. *Sedinia buettneri;* 2. *Cosymbia pupillaria;* 3 and 4. Beautiful Gothic, *Leucochlaena odites;* 5. and 6. Five-spot Burnet, *Zygaena trifolii;* 7. Three Humped, *Notodonta tritophus;* 8. Water carpet, *Lampropteryx suffumata;* 9. *Lampropteryx otregiata;* 10. Clear Underwing, *Sciapteron tabaniformis;* 11 and 12. Rannoch Looper, *Itama brunneata;* 13-15. Frosted Yellow, *Isturgia limbaria*

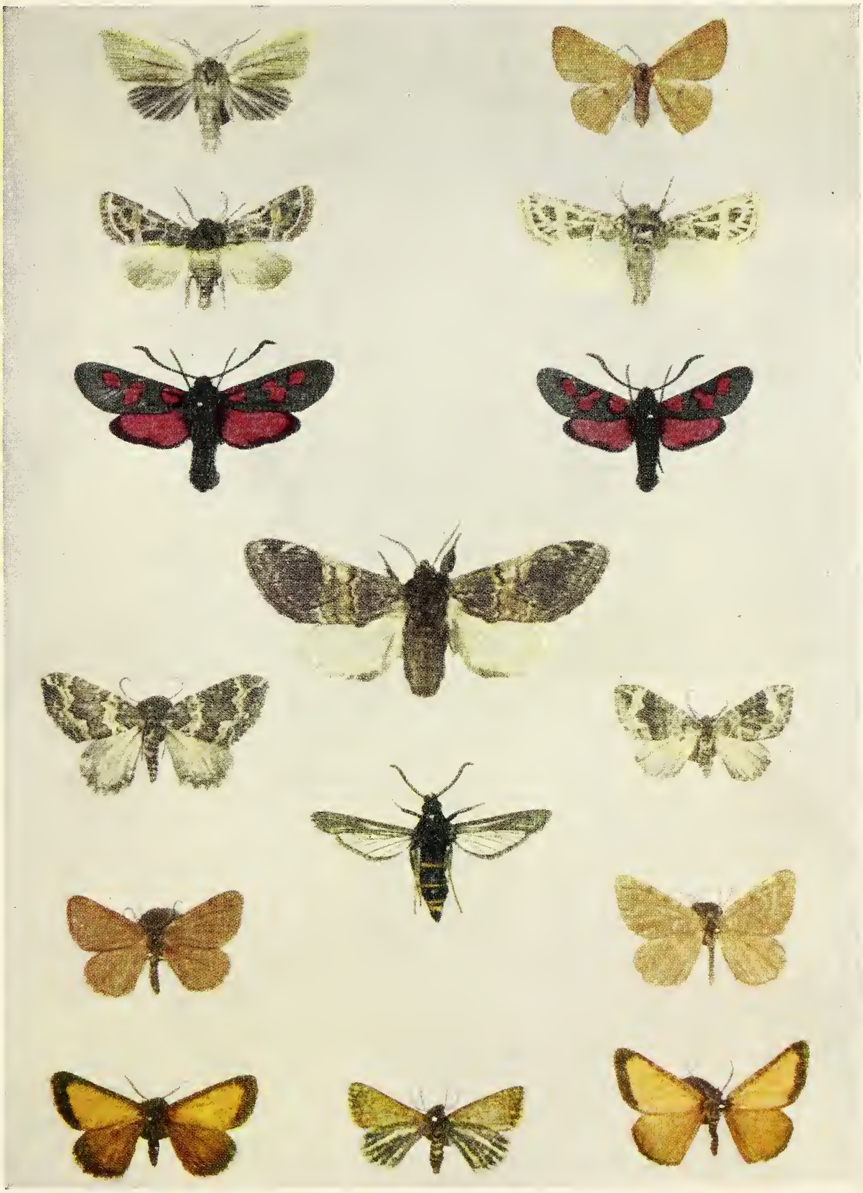

Plate 29

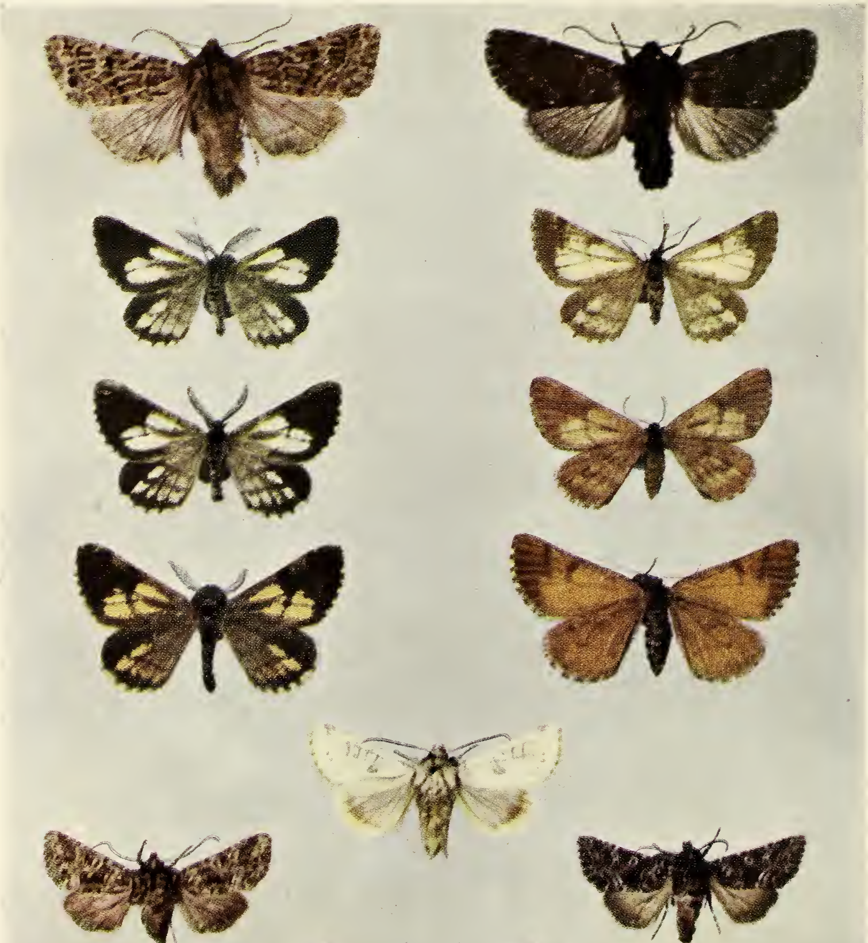

Plate 30

Plate 30. NORTHERN SPECIES AND ADJUSTMENT TO BACKGROUNDS

1
UNST
SHETLAND

2
RANNOCH

3
Male
TONGUE
SUTHERLAND

4
Female
TONGUE
SUTHERLAND

5
Male
ORTON
CUMBERLAND

6
Female
ORTON
CUMBERLAND

7
Male
NEW FOREST

8
Female
NEW FOREST

9
EASTBOURNE

10
CORNWALL

11
ISLE OF MAN

12
LEWES
SUSSEX

13
TORQUAY

14
OXSHOTT
SURREY

---

1. Northern Arches, *Xylophasia exulis;* 2. *Xylophasia assimilis;* 3-8. Bordered White, *Bupalus piniarius;* 3 and 4 var *inversa*, 5 and 6 Northern form, 7 and 8 Southern form; 9-11. Tawny Shears, *Hadena lepida;* 11. *capsophila* form; 12-14. Annulet, *Gnophos obscurata*

altogether beyond the confines of that subject, is chiefly responsible for breaking down the old distinction between the ' inexact ' and the ' exact ' sciences. Indeed, it is probable that in the near future many of the more obscure evolutionary problems will be clarified by that combination of population analysis, ecology, and genetics, which has proved so successful in recent years.

An example will indicate the scope of such work and the way in which it is being applied to moths. In order to describe the chief results of the rather extensive experiments involved, it is necessary only to amplify somewhat the information contained in Chapter 12 of *Butterflies*, a knowledge of which will be presumed. For the concept of natural selection is there explained and discussed, while the method of assessing animal populations by the marking, release and recapture of specimens is briefly described.

The investigation chosen to illustrate certain aspects of the experimental study of evolution has been conducted by some of my colleagues and myself from 1939 up to the present time. We have worked upon the Scarlet Tiger, *Panaxia dominula* L., Hypsidae, at Cothill in Berkshire where it inhabits a marsh of about fifteen acres; a photograph of this famous locality is shown on Plate XIX, figure 2. It is surrounded by woods and agricultural land unsuitable to this species, which is normally confined to swamps and river-banks where it feeds principally on Comfrey, *Symphytum officinale*. Thus the population is an isolated one. Moreover, as already explained (pp. 66-7), it is polymorphic, owing to the occurrence of the heterozygous form *medionigra* (Plate 11, figures 3 to 5) at a frequency too high to be maintained merely by mutation; as it appears to be elsewhere, for it is exceedingly rare outside this locality. *Medionigra* differs from the normal homozygote (Plate 11, figure 1; Plate 14, figure 1) in having the central white spot on the fore-wings reduced (figures 3 and 5) or absent (figure 4), while there is an additional black spot in the middle of the hind-wings. This may be quite conspicuous (figures 4 and 5) or it may consist of a few scales only (figure 3); thus it is decidedly variable. *Bimacula*, the rare homozygote corresponding to it, is shown in figure 2.

The Scarlet Tiger is single-brooded. The imagines, which are day-flying and very active in the sunshine, are to be found during the second three weeks of July. They have been studied quantitatively by the marking, release and recapture of specimens. For this purpose dots of cellulose paint, varying in colour and position, are used to indicate dates of capture, as described in *Butterflies*, pages 270-275, and one of the marked specimens withdrawn from the colony is shown on Plate 11, figure 1. The range of clearly distinguishable colours is considerable, and four positions are available for each of them: at the base or the tip of the fore-wing, and on the left or the right side. Consequently a large number of dates can be indicated in this way.

When a specimen is caught it is scored as normal, *medionigra* or *bimacula*. Thus the frequency of the three forms can be ascertained, for the mark which each insect receives before release ensures that it will not be counted for this purpose a second time.

One of the necessary steps in obtaining quantitative information on a colony of insects by the marking, release and recapture of specimens is to determine the average death-rate of the specimens studied (Ford, 1953c). Provided with this information, it is possible to estimate approximately how many individuals are added per day to the colony by emergence, or possibly by immigration into it, and how many are lost through death, or emigration from it; also the number of specimens flying at any given period and throughout the insect's whole season.

By these means it may, for instance, be possible to determine whether two forms of a species survive equally well in nature or whether one of them is being eliminated more rigorously than the other. In the latter event, it may be that one is at a relative advantage in some seasons and at a relative disadvantage in others. A survey of local conditions may reveal with what factors such a shift in survival-value is associated: it may prove to be correlated with alterations in population-size, with various climatic conditions, or with changes in the ecology of the habitat. Investigations of this kind bring us very close to the working of evolution.

It is probably true to say that by the use of such methods the Scarlet Tiger Moth at Cothill has been more thoroughly studied from a quantitative point of view than has any other wild population of animals upon earth. It has indeed provided the first practical test of a problem which has proved a storm-centre in modern biology, the relative importance of natural selection and of random survival in the evolution of small isolated or semi-isolated communities.

Owing to the simple working of the laws of Mendel, it would be possible to say whether or not changes in the relative frequency of a pair of allelomorphs can reasonably be ascribed to chance, if only we knew the size of the population concerned. Now the frequency of

Year	*dominula*	*medionigra*	*bimacula*	*Total*
1939	184	37	2	223
1940	92	24	1	117
1941	400	59	2	461
1942	183	22	0	205
1943	239	30	0	269
1944	452	43	1	496
1945	326	44	2	372
1946	905	78	3	986
1947	1244	94	3	1341
1948	898	67	1	966
1949	479	29	0	508
1950	1106	88	0	1194
1951	552	29	0	581
1952	1414	106	1	1521
	8474	750	16	9240

TABLE 2: Captures of three forms of the Scarlet Tiger at Cothill, Berkshire.

Year	*Gene-frequency per cent*	*Population size*
1939	9·2	?
1940	11.1	?
1941	6.8	2000 to 2500
1942	5·4	1200 to 2000
1943	5·6	1000
1944	4·5	5000 to 6000
1945	6.5	4000
1946	4·3	6000 to 8000
1947	3·7	5000 to 7000
1948	3·6	2600 to 3800
1949	2.9	1400 to 2000
1950	3·7	3500 to 4700
1951	2.5	1500 to 3000
1952	3·6	5000 to 7000

TABLE 3: The population-size of the colony of the Scarlet Tiger at Cothill, Berkshire, and the frequency in it of the *medionigra* gene.

the *medionigra* gene* at Cothill has indeed been determined each season from 1939 to 1952 inclusive, as shown in Table 3. Since such an estimate is so far unique, it may be of interest to examine the figures upon which it is based, and these are supplied in Table 2. Table 3 gives the approximate numbers of moths constituting the population from 1941 to 1952, calculated by the marking, release and recapture methods.

This work provided the first instance in which such information was available. It will be noticed that the gene-frequency fluctuates from year to year, and it is possible to calculate that such changes are too great to be due to chance; they must be the result of natural selection affecting the survival of the genotypes concerned (Fisher and Ford, 1947; Sheppard, 1951).

This conclusion is of considerable importance. It has been held by Sewell Wright in the United States of America and by his followers that 'genetic drift,' that is to say, random survival by which genes are spread or eliminated by chance, is of primary importance in the evolution of small isolated or semi-isolated populations. On the other hand, it has been contended, especially by Fisher, Sheppard and myself, that the effects of natural selection must overwhelm such random changes in all but very small populations, consisting of a few hundred individuals only, which are unlikely to be permanent. This work on the Scarlet Tiger is the first in which these contending views could be put to an experimental test, and it voted decisively against the concept of drift, which appears to be excluded also on theoretical grounds (Fisher and Ford, 1950; Sheppard, 1951). I should like here to pay a tribute to the painstaking and clear-sighted work of P. M. Sheppard who, subsequently to the original studies on the Cothill colony of *P. dominula* by Sir Ronald Fisher and myself up to 1947, took over and extended our investigations with conspicuous success.

As already indicated (pages 170-1), some form of geographical isolation appears to be an essential for the establishment of distinct races, so that the method by which evolution takes place in isolated colonies is a matter of crucial importance. It is to be noticed that in using the Cothill colony of the Scarlet Tiger we have taken advantage of the

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*This is expressed as the percentage of available loci that is occupied by the *medionigra* gene. That is to say, 50 per cent in a heterozygote and 100 per cent in a mutant-homozygote. Therefore if 18 per cent of the population were heterozygotes and 1 per cent were mutant-homozygotes, the gene-frequency per cent would be 10.

special qualities of balanced polymorphism, in which mutant forms occupy a considerable fraction of the population instead of appearing merely as great rarities. Thus the organism has an exceptional opportunity of adjusting itself to them.

It will be recalled that dominance-modification represents one aspect of such adjustment. This process was described in *Butterflies*, pages 257-62, with reference to the variety *lutea* of the Currant Moth, *Abraxas grossulariata* L., Selidosemidae, for this was the first instance in which such work was conducted on wild material. It is now possible to illustrate these experiments on *Abraxas* by means of specimens bred in the course of them. The species normally has a whitish ground colour (Plate 11, figure 6). The deep yellow mutant form *lutea* (figure 10) is a homozygote, while the heterozygotes, known as *semi-lutea*, are of an intermediate pale yellow shade (figure 8). Thus all three genotypes are visibly distinct. By breeding for four generations from the more and the less extreme forms respectively of the heterozygotes, it was possible to make *semi-lutea* nearly a dominant in the one line (figure 9) and nearly recessive in the other (figure 7). It was shown that the gene itself had not been changed, as it would have been by picking out various members of a multiple allelomorph series, but rather the response of the organism to that gene. This was demonstrated by crossing the modified heterozygotes to unrelated wild specimens when, after two generations, the original expression of *semi-lutea* was largely restored.

Similar experimental results have been obtained with the *medionigra* form of the Scarlet Tiger, which is very suitable for such work since the heterozygotes are also distinguishable. Being a polymorphic condition with a high frequency in the population, there was clearly some possibility that a corresponding adjustment to that obtained in the laboratory might be detected in the field within a number of generations small enough to be studied by direct observation, and of this there is now evidence. It is so far a unique experience to evoke an evolutionary change by the simple and efficient methods of the laboratory and then to see it reproduced, though slowly and feebly, by the bungling ineptitude of the forces of nature.

It has already been pointed out that H. B. D. Kettlewell has obtained evidence that a similar type of change has taken place in the *carbonaria* form of the Peppered Moth, *Biston betularia* L., Selidosemidae, which has only become completely dominant since its first appearance in the middle of the last century. That change has not yet been produced in the laboratory, but it is not difficult to see that the original expression of the gene may well be restored by an appropriate experimental technique: a test which is, in fact, soon to be made. Here indeed we have evidence, already used in discussing rural melanism in Chapter 13, that the spread of single ' major ' genes may necessitate various adjustments in the gene-complex, as demonstrated by Timofeeff-Ressovsky (1940) in the ladybird, *Epilachna chrysomelina* F. It is a noteworthy aspect of the recent success of melanic forms in moths that this, the most spectacular instance of evolution ever actually witnessed, should involve the spread of single ' major ' genes; for selection operates more effectively on multifactorial than upon unifactorial characters.

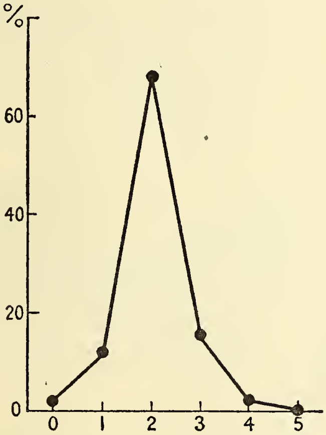

FIGURE 4

The distribution of spotting per hind wing in the males of the Meadow Brown Butterfly

In writing on butterflies I saw no objection to drawing occasional examples from moths, and here the reverse procedure can usefully be adopted: for it will be helpful at this point to discuss the ecological and evolutionary work on a multifactorial character now being conducted on the Meadow Brown butterfly, *Maniola jurtina* L., Satyridae (figured in *Butterflies*, Plate 41). Nor is the use of such material inappropriate in the last chapter of what is effectively a two-volume work on the British Macro-Lepidoptera as a whole.

It is a singular fact that some of the remarkable attributes of the commonest species may pass unobserved by generations of collectors. The Meadow Brown is one of the most familiar butterflies in England, yet it has not until lately been observed that the distribution of

Plate 31. MELANISM: INDUSTRIAL AND NON-INDUSTRIAL

1
THURSBY
CUMBERLAND

2
(EXPERIMENTAL MATERIAL)

3
SOMERSET

4
LONDON

5
THURSBY
CUMBERLAND

6
(EXPERIMENTAL MATERIAL)

7
Male
CUMBERLAND

8
Male
S. YORKSHIRE

9
FEMALE
TORKIN
CUMBERLAND

10
THURSBY

11
OXFORDSHIRE

12
fully grown larva
NEW FOREST

13
fully grown larva
CHINGFORD
ESSEX

1 and 2. Early Thorn, *Selenia bilunaria;* 3 and 4. August Thorn, *Ennomos quercinaria;* 5 and 6. Engrailed, *Ectropis bistortata;* 7-9. Pale Brindled Beauty, *Phigalia pilosaria;* 10-13. Green-brindled Crescent, *Allophyes oxyacanthae*

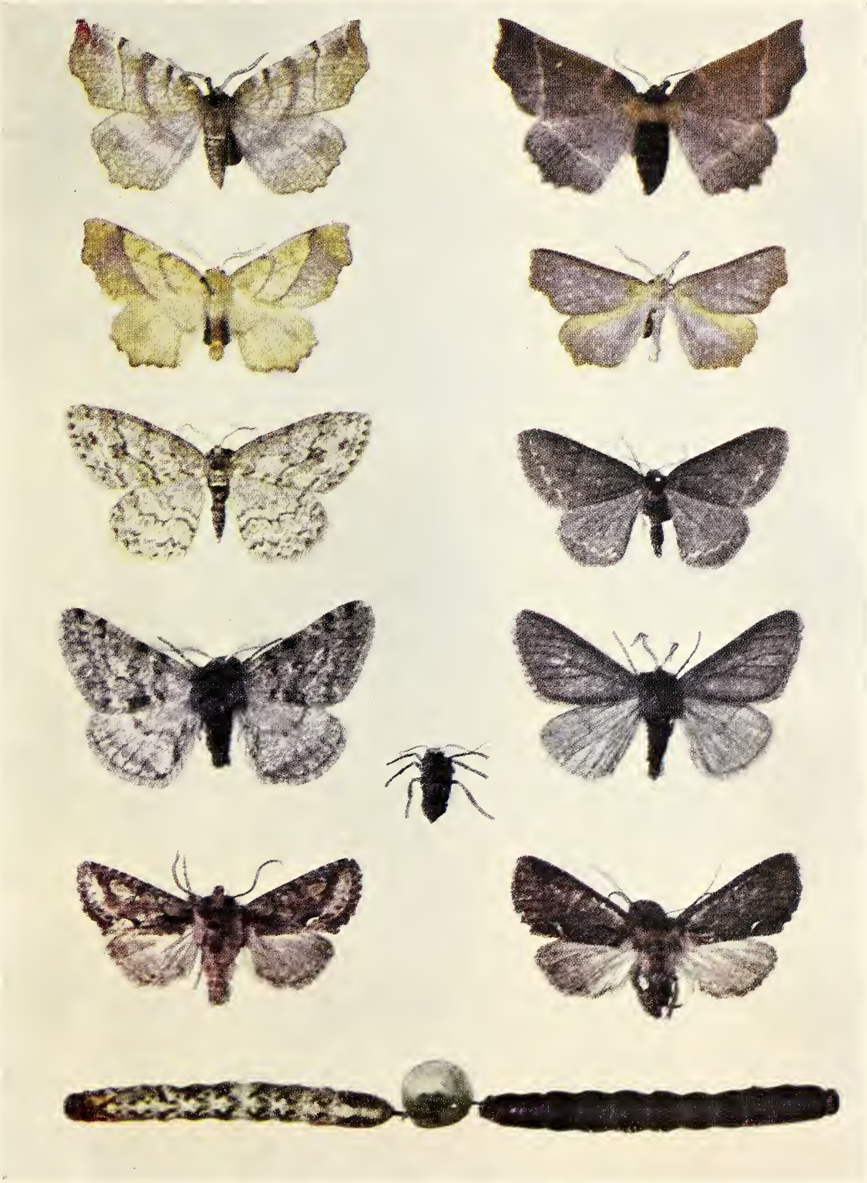

Plate 31

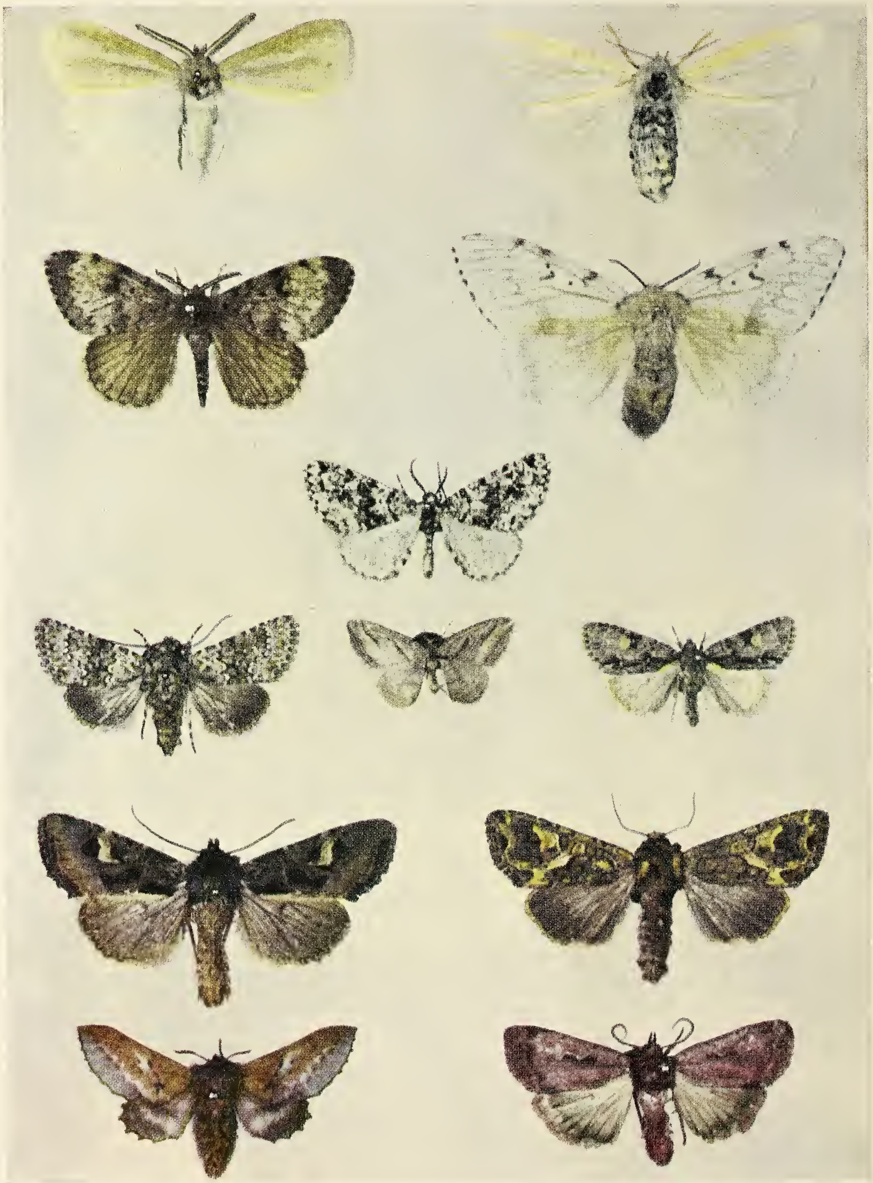

Plate 32

1
Male
(*no data*)

2
Female
WICKEN

3
Male
(*no data*)

4
Female
(*no data*)

5
(*no data*)

6
COLCHESTER

7
(*no data*)

8
CAMBRIDGE

9
SUSSEX

10
CAMBRIDGESHIRE

11
(*no data*)

12
(*no data*)

1 and 2. Reed Tussock, *Laelia coenosa;* 3 and 4. Gipsy Moth, *Lymantria dispar;* 5. Speckled Beauty, *Cleora arenaria;* 6. Small Ranunculus, *Hadena dysodea;* 7. Many Lined, *Euphyia polygrammata;* 8. Marsh Dagger, *Apatele strigosa;* 9. Flame Brocade, *Trigonophora flammea;* 10. Orache Moth, *Trachea atriplicis;* 11. Small Lappet, *Epicnaptera ilicifolia;* 12. Rosy Marsh Moth, *Caenophila subrosea*

spotting on the underside of the hind-wings is of an exceptional nature and presents problems of unusual interest.

The spots vary in number from 0 to 5. Their frequencies are quite different in the two sexes and in the female they provide a sensitive indication of evolutionary divergence. The general type of male spotting is everywhere the same throughout southern England and the Isles of Scilly, having a mode (or maximum) at 2 spots, from which the frequencies fall away on either side (figure 4). On the other hand, in the southern counties, from West Devon to East Suffolk, females with no spots are much the commonest, while those with higher numbers become progressively rarer, so that the frequencies much resemble one half of the male distribution (figure 5). However, in East Cornwall, and extending across the county boundary to Tavistock and Plymouth in Devon, female spotting is bimodal, with a larger mode at 0 spots and a smaller one at 2 (figure 6). Two populations in the Falmouth area proved to be consistent with one another but distinct from the East Cornish group, the number of specimens with 0, 1 and 2 spots being nearly the same. On the very distinct Land's End Peninsula, female spotting is so altered that its distribution resembles the male type, with a single mode at 2 spots.

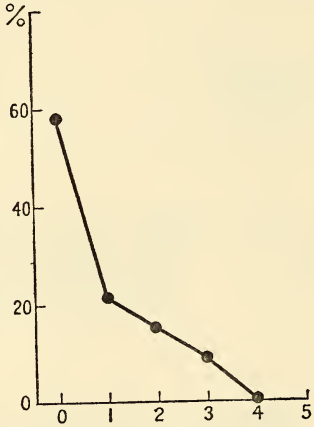

FIGURE 5

The distribution of spotting per hind wing in females of the Meadow Brown Butterfly in Southern England, excluding Cornwall

These facts merit some consideration. On the one hand, the character in question, the distribution of female spotting, is evidently capable of wide variation. Yet its uniform nature from Devon to Suffolk was established by samples collected in a number of widely scattered localities. These gave strictly consistent results, although the area involved is extremely diversified: it includes the greatest differences in temperature and rainfall to be found in Britain, while some of the places where the specimens were collected were on alkaline and others on neutral or acid soil, a distinction which has a profound effect upon the vegetation and ecology of the district. The results were similar in successive years, so we cannot escape the conclusion that the arrangement of female spotting is stabilised by selection, which thus over-rides the effects of great environmental differences.

The alteration in spot-frequency from the Devon to the East Cornish types is quite remarkable. All the samples taken within the area of each agree with one another; yet Lydford, Devon and Lewannick, Cornwall, where the localities tested approach most nearly, are only fourteen miles apart. It was not possible to examine collections from the intervening country owing to the difficulty of obtaining sufficient numbers. The division between the two groups falls near the county boundary which for a considerable distance approximately separates Carboniferous and Devonian rocks. This places them in regions which are to some extent geologically distinct. The species fails to respond to differences far greater than this across southern England, but it apparently becomes ' sensitized ' to slight environmental effects in the south-west. We have found that small ecological barriers are effective isolating agents in this insect, and a locality five miles east of Plymouth, but cut off from the west by the estuary of the Yealme, has completely

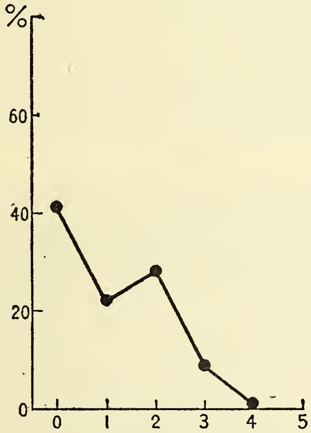

Figure 6

The distribution of spotting per hind wing of females of the Meadow Brown Butterfly in East Cornwall the characteristics of the eastern races, not of that inhabiting the Plymouth area.

The Land's End Peninsula consists, like Bodmin Moor and Dartmoor, of a granite intrusion and there the Meadow Brown is moderately common, though it is very rare on the east side of the isthmus which separates that district from the rest of Cornwall. Thus the very distinct colony at the west end of the county is an isolated one, and samples taken from the north and south coasts were almost identical.

The qualities for which the Meadow Brown population is rigorously selected must be other effects of the genes responsible for controlling the spot-distribution of the females. These presumably are of a physiological nature.

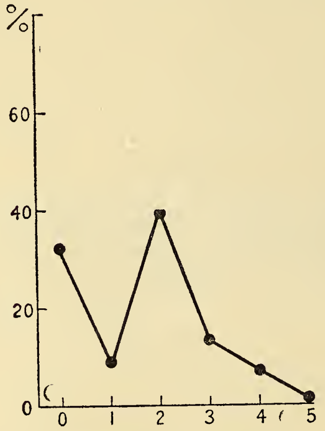

FIGURE 7

The distribution of spotting per hind wing of females of the Meadow Brown Butterfly on Tean, Isles of Scilly, (areas 1 & 3, 1951)

W. H. Dowdeswell and I, who are responsible for this work, find the situation in the Isles of Scilly to be particularly revealing. We have studied the spotting of the Meadow Brown on three 'large' and numerous 'small' islands. These differ markedly in size, each of the large islands being at least seventeen times the area of any of the small ones. Female spotting takes very different values on the small islands: thus it may be bimodal with the larger mode at 2 and the smaller at 1, or the reverse (figure 7), or unimodal with a single mode at 2. However, its distribution is the same, with frequencies approximately equal for 0, 1 and 2 spots, on the three large islands of Tresco, St. Martin's and St. Mary's, although they lie far apart. Moreover, St. Martin's is separated from the other two by small islands on which the spotting

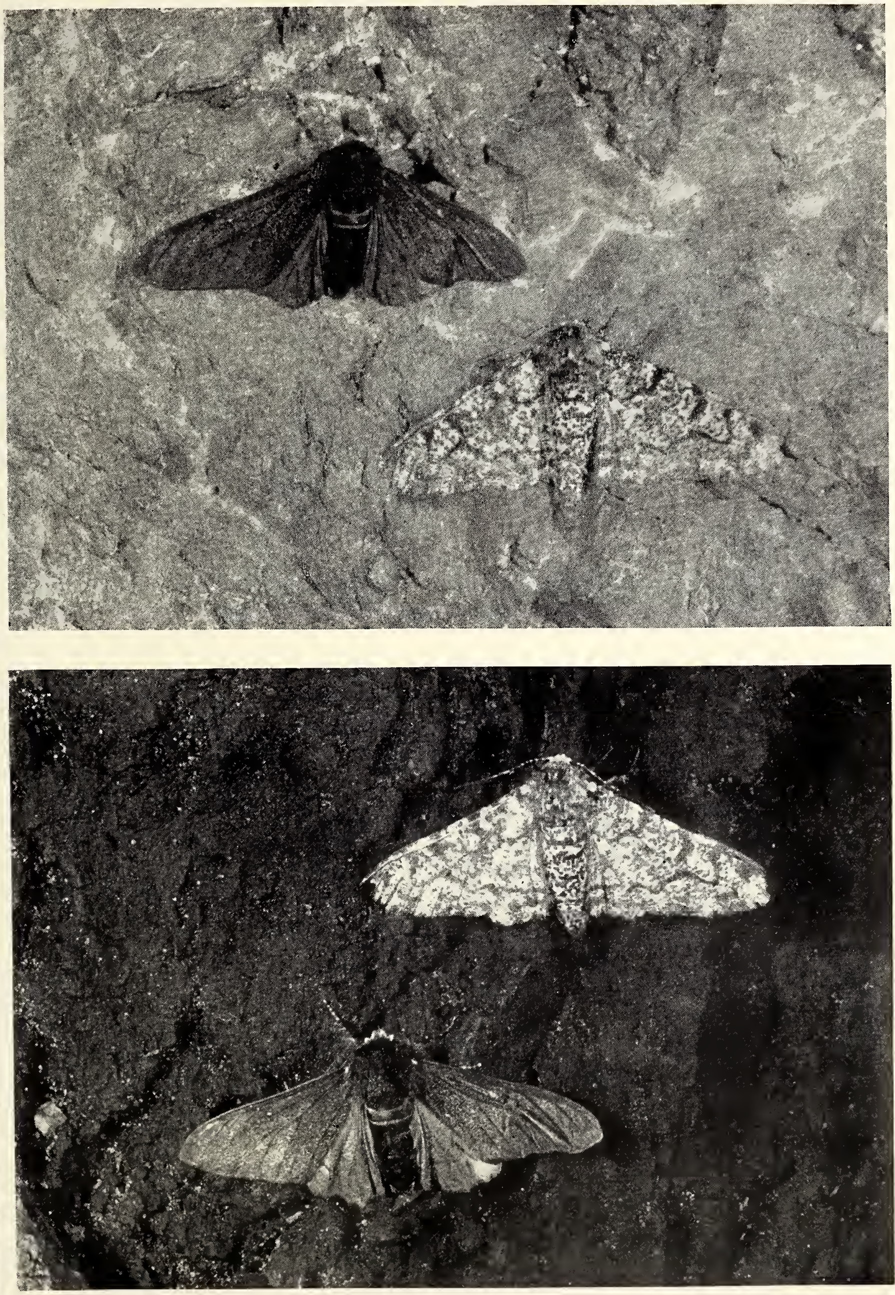

Plate XXIII. Industrial Melanism in the Peppered Moth, *Biston Betularia*
1 (*above*). Normal and Melanic specimens on clean bark; 2 (*below*). Normal and Melanic specimens on sooty bark

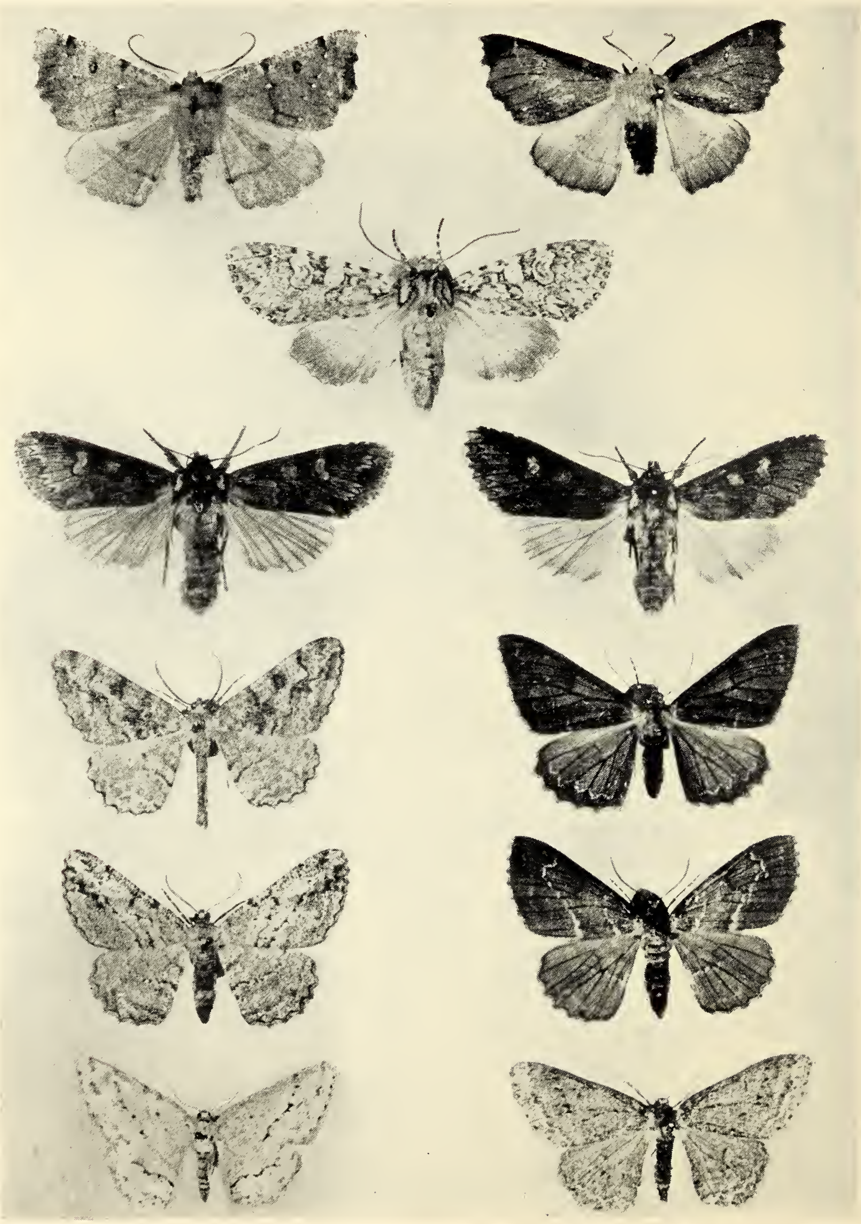

Plate XXIV

1
THURSBY

2
MANCHESTER

3
ORTON
CUMBERLAND

4
DELAMERE
CHESHIRE

5
DELAMERE
CHESHIRE

6
BERKSHIRE

7
LANCASHIRE

8
(EXPERIMENTAL MATERIAL)

9
KENT

10
THRUSTONFIELD
CUMBERLAND

11
DELAMERE
CHESHIRE

1 and 2. Scalloped Hazel, *Gonodontis bidentata;* 3-5. Grey Arches, *Polia nebulosa;* 3. typical, 4. melanic heterozygote, 5. melanic homozygote; 6 and 7. Mottled Beauty, *Cleora repandata;* 8 and 9. Willow Beauty, *Cleora rhomboidaria;* 10 and 11. Small Engrailed, *Ectropis crepuscularia*

is quite different. Consequently the similarities cannot be due to migration (Dowdeswell and Ford, 1953).

Three types of explanation can be advanced to account for the close correspondence of spotting on the large islands and its diversity on the small ones. (1) The random survival of specimens (" genetic drift ") which, as already stated, can be effective in very small groups of a few hundred individuals but not in large ones. In fact, however, the populations on some of the small islands comprise many thousands, and are much too large for such a concept to be applicable to them. (2) It may be that the Meadow Brown on Scilly has been reduced in numbers at some period in the past. This might have left the small islands almost uninhabited, to be repopulated from a few individuals whose chance characteristics might determine those of the communities derived from them. The large islands, on the other hand, might well carry a sufficient population for the butterflies on them to survive such a fluctuation unchanged. However, we have evidence that such elimination is not a requisite for the production of the observed variation from island to island, for the butterfly exists in three isolated colonies on the small uninhabited island of Tean which we have studied intensively. One of these has altered significantly during our own observations of it, during which no such fluctuation has taken place. (3) I believe the correct explanation of this curious situation depends upon the fact that populations isolated in small areas can each adjust themselves to the special characteristics of their habitats, while those living in an extensive tract of country, such as a large island, can only be adapted to the average of the conditions found there. This is the reason why the subdivision of a community into small isolated groups favours its rapid micro-evolution. Moreover, it may ultimately lead to the formation of new subspecies and eventually of species; for genes interact with one another to produce their effects so that selection, fitting the organism to different habitats, may sooner or later alter the balance of the sex-determinants and so give rise to partial, and finally to total, sterility (pages 40-3). In addition, as explained in Chapter 12, when two isolated races become adapted to different environments, they may preserve their identity should they subsequently extend their ranges and meet. Even if still fully fertile, they are then committed to paths which, if they survive, will lead them to become separate species.

EXTINCTION

Evolution is far more often a failure than a success, and the vast majority of evolving lines are committed inevitably to extinction. There are many reasons for this, but it will suffice to mention two of them. First, natural selection tends to fit an organism more perfectly to its environment. Thus, because in the process it becomes increasingly adjusted to one set of conditions, the types of variation which it can usefully employ become progressively restricted, and so does the possibility of pursuing evolutionary courses other than the one it has already adopted. Environments, however, are not permanent; sooner or later they will change, and those species too closely adapted to them will be unable to readjust themselves and must perish. Secondly, natural selection has been defined as ' the survival of the fittest '; that is to say, the *individuals* which are best suited to their environment will tend to contribute more to posterity than those that are less well endowed and, in so far as the qualities concerned are inherited, they will by this means be spread through the population. But what is good for the individual is not necessarily good for the race and may even tend to destroy it. Thus specimens of exceptionally large size are often at an advantage in colonies or herds; but it is a dangerous thing to alter the size of an organism, since the phenomena of relative growth (page 7) make it likely that this will change not merely the bulk but the proportions of the body, which will have been carefully adjusted to the animal's needs.

Lepidoptera are subject to quite different types of risk according to whether they are widespread and occupy rather varied country, restricted to a particular kind of habitat such as moorland or fen, or so exceedingly localised that the destruction of one or two small areas would be fatal to their survival in Britain. As pointed out in *Butterflies*, Chapter 7, some species are affected by extreme, and probably recurrent, fluctuations in numbers. If they are abundant, they may carry a sufficiently large population for these to place them in no jeopardy even when their range is restricted and they become rare. If, on the other hand, they are uncommon, they may be unable to survive their period of minimum density, though could they but have maintained themselves for a few seasons longer they might have been temporarily out of danger.

There are in fact two types of such fluctuations to be considered, local and generalised. The local one affects isolated colonies independently, and it is often far greater in degree than is appreciated by those biologists who have not made quantitative studies of animals in the field. It is indeed not uncommon to find a colony of a butterfly or moth oscillate from one numerical extreme to another in a short time. An instance of this was given, and its evolutionary effects discussed, in *Butterflies*. It was pointed out that in a period of five generations an isolated community of the Marsh Fritillary passed from the condition in which only half a dozen specimens or so could be obtained as the result of a day's work to that in which the collector was surrounded by a pullulating cloud of the insect, and that this allowed it to undergo a minor evolutionary change with great rapidity.

On the other hand, generalised fluctuations in numbers affect certain animals and plants over the whole country. They may also enable a species to adjust itself to its environment, or they may bring it to extinction. It would be useful to examine that aspect of evolution by analysing the causes which have within the last hundred years or so led to the destruction of certain British moths. Their number is, unfortunately, considerable, and it will be worth while to discuss only a few of them, choosing those which illustrate certain types of danger which threaten our Lepidoptera to-day. R. F. Bretherton (1951) has given an excellent review of our lost butterflies and moths to which I am much indebted in preparing this account, and I recommend it to those who require more detailed information on them.

Many species both of butterflies and moths became scarce from about the middle of last century. Some were affected earlier and some later, but there has now been a gradual reversal of the process and their numbers have very generally increased from about the First World War onwards, in spite of the destruction of woodlands, and the extension of industry, agriculture and housing, which has taken place during that period. These changes seem to be correlated with long-term climatic effects, as indicated by the extension and retreat of the Scandinavian glaciers, and a slight average increase in winter temperatures during the last forty years or so.

The widespread reduction in numbers of our butterflies and moths to which attention has just been drawn seems in itself to have been sufficient to bring a few species to extinction. A good example is provided by the Small Ranunculus, *Hadena dysodea* Schiff., Caradrinidae (Plate 32, figure 6). This was affected late in the period of decline, for up to 1900 it was widespread in the southern and especially the eastern counties, being frequent in East Anglia and Essex and common in Cambridgeshire, where it was sometimes even a pest upon lettuce crops. The insect had been known from the early days of entomology, yet by the end of the first war it had become practically extinct. The last captures within its normal range were a few taken in Essex in 1918, and only four specimens have been reported since. One writer in 1903 says that the particular variety of lettuce which it favoured was by that time little cultivated so that the moth had become scarcer. Yet it will feed upon wild lettuce, and it is probable that the reduction in numbers to which he refers was unconnected with the food-plant. Neither over-collecting nor human interference with the countryside can be responsible for the decline of this insect. It may possibly have suffered from a virus or other disease at the time when its numbers were much reduced during one of its regular long-term fluctuations and that the two effects operating together were fatal to it. We have indeed no recorded evidence of such infection, which might, however, have been serious without attracting attention.

The loss of the Speckled Beauty, *Cleora arenaria* Hufn., Selidosemidae (Plate 32, figure 5), though taking place at an earlier date, appears to be a parallel instance in the sense that it seems to be unconnected with human interference. The moth was discovered in 1822. It inhabited the tops of oak trees in the New Forest, and it apparently existed also, but was rarer, in Tilgate Forest, Sussex. The larva fed upon lichens. The insect continued to be taken regularly up to about 1872 but nothing has been heard of it since, except for one specimen in the New Forest in 1898 and a few scattered records from Sussex prior to 1905. Its loss long before there was extensive tree-felling in its haunts must presumably be attributed either to disease or to an unusually severe fluctuation in numbers. The history of the Small Lappet, *Epicnaptera ilicifolia* L., Lasiocampidae (Plate 32, figure 11), is somewhat similar. It is a bilberry feeder, and occurred at Cannock Chase and on a few moors in Shropshire and Yorkshire. Some of these are unchanged, but it has not been seen for forty years.

Human interference appears to be principally responsible for the loss of some of our Fenland moths, though this may be indirect as well as direct. The Reed Tussock, *Laelia coenosa* Hb., Lymantridae (Plate 32, figure 1 male and 2 female), was exclusively an insect of the Fens. It was discovered at Whittlesea in 1819 and was abundant both there and at Yaxley and Burwell until these were drained and turned into agricultural land in the middle of the last century. It was also common at Wicken, which still remains a Fen, until about 1860, but subsequently grew scarce. My friend F. C. Woodforde told me that he found the larva not uncommon there in 'the late sixties or early seventies,' but the last capture appears to have been made in 1879 and the insect is certainly extinct in Britain.

The little Many-lined Moth, *Euphyia polygrammata* Bork., Hydriomenidae (Plate 32, figure 7), was first reported as British in 1831. It was common at Burwell Fen until that was drained about 1850. Although it used to occur also between Upware and Wicken villages in sites which I suppose are not greatly altered, and in Wicken Fen itself, though uncommonly, it has not been seen since about 1880.

The history of the Gipsy Moth, *Lymantria dispar* L., Lymantridae (Plate 32, figure 3 male, 4 female), is obscured by the repeated introduction of foreign specimens. However, it was probably indigenous and was quite abundant in some of the Fens, where it was discovered in 1820, though it had been known as a British species long before that. It existed also in the Norfolk Broads. Many of its haunts have been destroyed, though a few remain. However, R. South writing in 1892 says, 'somewhere about the fourth decade the species began to decrease in numbers and towards the end of the fifties it had practically ceased to exist as a wildling.' There have in later years been records of single specimens in several parts of the south of England, and Mr. S. Beaufoy found a larva, which he successfully reared to produce a male moth, near Chattisham, Suffolk, in 1948. But the insect is often bred in this country from foreign parentage and no great significance can be attached to these stray captures. Abroad it is by no means restricted to fens and marshes.

The last three moths are all species whose haunts have been greatly reduced, though not wholly destroyed, by the drainage of the Fens. It is clearly pertinent to ask why they do not survive in such of their former localities as still exist. I think there are two answers to that question. First, if they did so, the area they would inhabit would be but a minute fraction of what it was in the past; and, as already indicated, insects reduced to very small populations are in great danger if subject to fluctuations in numbers. Secondly, as Bretherton points out, the drainage of a great area of the Fens must have had important consequences upon the remnants which remain. It must have caused local climatic changes, so that Fenland is probably drier in winter, hotter in summer, and less subject to mist than it was a century ago. Owing to the lowering of the water-table and the drying of the whole area, the ecology of the remaining Fens, such as Wicken and Woodwalton, is becoming modified and scrub is tending to oust the true fen plants. Bretherton is certainly right also in pointing out that land reclamation has caused an alteration in the bird population, concentrating the true fenland species into very small areas and causing those normally found along hedgerows and in agricultural land to colonise the Fens, so adding to the hazards experienced by the insects which inhabit them. Such changes may well prove fatal to species which are rather accurately adjusted to this specialised environment.

Such indirect human interference consequent upon extensive drainage is probably responsible at least in part for the extinction of several moths which frequented Fenland but not the Fens themselves. Thus the Orache Moth, *Trachea atriplicis* L., Caradrinidae (Plate 32, figure 10), was found in the meadows adjoining them and its haunts are still available for it, though doubtless somewhat altered in climate and ecology. It was widespread in Cambridgeshire and Huntingdonshire and occurred in much smaller numbers in the neighbouring counties; but it had become rare in the 1890's, and the last specimens to be taken in Cambridgeshire were caught in 1910 and in Huntingdonshire in 1905. The history of the Grizette, *Apatele strigosa* Schiff., Caradrinidae (Plate 32, figure 8), is rather similar, for it too was principally found not in the Fens but in their neighbourhood. It was always rare but the captures this century seem to have been reduced to occasional specimens, and there have now been no records for about twenty years. In the past it has occurred singly here and there in other parts of England; but if this indicated the existence of small scattered colonies, nothing has been heard of them for a long time and they may have perished in a general decline in the numbers of the Grizette.

At least one Fenland species has disappeared owing to the total destruction of its haunts. This is the Rosy Marsh Moth, *Caenophila subrosea* St., Caradrinidae (Plate 32, figure 12), which was discovered in 1827. It was found plentifully in the Whittlesea area but not elsewhere, and remained so until this was drained in 1850, after which it was never seen again.

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APPENDIX

CLASSIFICATION

An account of the classification of Insects, and of the British Butterflies in particular, has been given in the previous volume of this work (*Butterflies*, Chapter 4), in which the fundamental characteristics of the Lepidoptera were also described in some detail (Chapters 2 and 3). This Appendix is therefore intended merely to provide some information on the Families, Superfamilies and Suborders to which the species mentioned in this book belong.

Both the classification and the nomenclature adopted here are, with few exceptions, those of Kloet and Hincks (1945), while the diagnostic features of the various groups are condensed from Meyrick (1927), and Imms (1942), together with the addition of some further facts. The structure of the frenulum is discussed in the first chapter of this book. The other anatomical characters that are mentioned have been described in *Butterflies*, where the neuration of the wings, and the system of numbering the nervures, is explained by means of a diagram (figure 2 on page 36).

No attempt is here made to provide a full account of the various Families, and higher taxonomic divisions, of the Lepidoptera. On the contrary, a few of their features only are given, sufficient to suggest the general structure and appearance of the moths assigned to them.

This will be assisted by reference to the Plates, on which are shown large numbers of species belonging to nearly all the groups mentioned in the text. Moreover, illustrations of one or two characteristic examples of each family are cited in the Tabulation which follows, many of them in their earlier as well as in their imaginal stages. It would thus be a mistake to judge this as a precise classification of the Order. It is rather a guide to the relationships of the moths included in this book.

Taxonomy has suffered from a failure to keep in touch with modern advances in biology. In the Lepidoptera, criteria of the various classificatory divisions are, with but few exceptions, limited to features which can be studied by inspecting small numbers of the early stages and dried specimens preserved in museums. Even the data so obtained have rarely been treated statistically, a quite essential requirement, while genetic, cytological, physiological and chemical methods have hardly yet been used to elucidate the systematics of this Order. In the circumstances, therefore, it is necessary here to employ the conventional standards of classification, while pointing out the necessity of extending them.

The Order Lepidoptera is divided into 3 Suborders, 13 Superfamilies and 64 Families. The butterflies comprise one of these Superfamilies. The remainder of the Lepidoptera are moths, and the species with which this book is concerned belong to 2 of the Suborders, 8 of the Superfamilies and 23 of the Families.

ORDER LEPIDOPTERA

SUBORDER	Homoneura. Neuration of fore- and hind-wings similar. Jugum on fore-wings. No frenulum. Nervure 1c present.
Family	Hepialidae (Swift Moths). Proboscis absent. Maxillary palpi obsolete, the tibiae without spurs. Larva: 10 to 16 prolegs or with the prolegs lost. Pupa: one or two basal abdominal segments fixed. ('Common Swift': Plate X, figure 6; Plate XVI, figure 1; Plate IX, figure 1; Plate VII, figure 4; 'Ghost Moth': Plate 28, figures 1 to 5).
SUBORDER	Heteroneura. Neuration of fore- and hind-wings different. Frenulum usually present. Nervure 1c present or absent on hind-wings.
SUPERFAMILY	Caradrinoidea. Maxillary palpi rudimentary or absent. Frenulum present. 1c absent from both fore- and hind-wings. Fore-wings: 5 arises close to 4. Pattern: five transverse lines and three discal spots. Larvae may be very hairy. Usually 10 prolegs, but those on 7th and 8th segments sometimes absent. Pupae with segments 9 to 11 free. Not protruded from cocoon at emergence.
Family	Arctiidae (Tiger Moths). Proboscis more or less developed. Posterior tibiae with all the spurs present. Typical wing markings generally not distinctly traceable. Thorax and abdomen: hairy or smooth beneath. Eggs, spherical and nearly smooth. Larvae, hairy with 10 prolegs.

Pupae, in a cocoon above ground, constructed of silk and larval hairs.
(' Garden Tiger ': Plate 22, figures 1 and 2; Plate 9, figures 5 to 7; ' Muslin ': Plate 10, figures 7 to 10; ' Dingy Footman ': Plate 13, figures 3 and 4).

FAMILY Hypsidae.
Thorax hairy beneath, abdomen smooth.
Proboscis well developed.
Fore and hind-wings: nervure 5 originates near angle of cell.
Eggs spherical, larvae hairy, cocoon very slight.
(' Scarlet Tiger ': Plate XI, figure 4; Plate 15, figure 1).

FAMILY Nolidae.
Proboscis well developed.
Fore-wings with three sub-costal tufts of scales.
Eggs ribbed, larvae with tufts of hair and no prolegs on 7th segment.
Pupae in a boat-shaped cocoon, imagines small.
(' Short Cloaked Moth ': Plate XVI, figure 6; Plate VII, figure 2).

FAMILY Cymbidae.
Proboscis developed.
Many species possess green pigment changed to brown by an alkali.
Larvae with 10 prolegs, not hairy.
Pupae in boat-shaped cocoon.
(' Green Silver Lines ': Plate X, figure 1, Plate 16, figure 1).

FAMILY Caradrinidae (" Noctuid " Moths).
Proboscis usually well developed.
Thorax very hairy beneath.
Hind-wings: nervure 5 absent or imperfect.
Eggs spherical ribbed, or netted.
Larvae with 10 prolegs, usually with few hairs.
Pupae usually subterranean.
About 6,000 species, mainly in temperate regions.
(' Turnip Moth ': Plate 5, figure 5; ' Grey Dagger ': Plate 17, figures 14 and 16; ' Small Dark Yellow Underwing ': Plate 27, figure 15).

FAMILY Plusiidae.
Proboscis well developed.
Fore-wings relatively broader than in Caradrinidae, body more slender.
Hind-wings: nervure 5 well developed.

Eggs spherical, ribbed or netted.
Larvae with few hairs. Sometimes prolegs on 7th or 8th segment absent or rudimentary.
Pupae usually in cocoon above ground.
Principally a tropical family.
(' Silver Y ': Plate 16, figure 4; ' Red Underwing ': Plate 5, figure 1; ' Waved Black ': Plate 4, Plate XI figure 2).

FAMILY Lymantriidae (Tussock Moths).
Proboscis short, generally rudimentary.
Male antennae bipectinated to the tip.
Hind-wings: nervure 5 present.
Eggs spherical and smooth; larvae hairy, with dense tufts.
Pupae hairy, in cocoon above ground.
(' Gold Tail ': Plate 24, figures 1-4; Plate IX, figures 3 and 4; ' Gispy Moth ': Plate 32, figures 3 and 4).

SUPERFAMILY Notodontoidea.
Maxillary palpi absent.
Fore-wings: 1c absent, 5 no nearer 4 than 6.
Hind-wings: 1c absent. Frenulum nearly always present.
Pupae: segments 9-11 free, not protruded from cocoon on emergence.

FAMILY Sterrhidae (The Waves).
Proboscis developed.
Fore-wings: 11 connected with 9, 10 springs from 9.
Hind-wings: 5 fully developed.
Eggs oblong and reticulated.
Larvae elongated and slender. Few hairs. Prolegs 7-9 absent.
Pupae in slight cocoon above ground.
(' The Blood Vein ': Plate 16, figure 5; ' Weaver's Wave ': Plate 26, figure 5; ' Portland Ribbon Wave ': Plate 26, figure 16).

FAMILY Geometridae.
Proboscis well developed.
Most species coloured green by a pigment converted to brown by an acid.
Fore-wings: 11 free from 9, 10 arising from 9, 5 fully developed.
Early stages=those of Sterrhidae.
(' Common Emerald ': Plate 1, figure 4).

FAMILY Hydriomenidae (Carpets and Pugs).
Proboscis well developed.
Fore-wings : 10 arises separately, fusing with 11 and 9, or arises from 11 and fuses with 9, 5 present and fully developed.
Eggs rather flattened and reticulated.
Larvae slender. No prolegs on 7 to 9.
Pupae usually subterranean.
(' Mottled Pug ': Plate VII, figure 3; ' Marbled Carpet ': Plate 13, figures 12-14; ' Water Carpet ': Plate 29, figure 8).

FAMILY Brephidae.
Proboscis sometimes developed sometimes degenerate.
Hind-wings: 5 present.
Eggs smooth. Larvae: prolegs on 7, 8 and sometimes 9 rudimentary.
Mainly an Australian family.
(' Orange Underwing ': Plate 2, figure 6; Plate VII, figure 1; ' Rest Harrow ': Plate 3, figure 5).

FAMILY Selidosemidae.
Proboscis usually well developed, sometimes rudimentary.
Fore- and hind-wings: 5 imperfect (not tubular) or absent.
Eggs rather elongated, reticulated or ribbed.
Larvae slender. No functional prolegs on 7, 8 and usually 9.
Pupae subterranean or in slight cocoon above ground.
(' Peppered Moth ': Plate 19, figure 3; Plate XXIII; ' Scalloped Oak ': Plate 8, figures 1 and 2; ' Black Mountain Moth ': Plate 27, figures 10 to 12).

FAMILY Polyplocidae.
Proboscis well developed.
Thorax hairy below. Hind-wings: 5 developed.
Eggs netted. Larvae stout; all prolegs developed.
Pupae in slight cocoon above ground.
(' Yellow Horned ': Plate VIII, figure 2; Plate 25, figure 1.)

FAMILY Sphingidae (Hawk Moths).
Proboscis very long or sometimes imperfect.
Thorax hairy beneath.
Hind-wings: 5 present.
Eggs smooth; larvae stout, usually with posterior horn.
Pupae subterranean.
Imagines large with powerful flight.

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No attempt is here made to provide a full account of the various Families, and higher taxonomic divisions, of the Lepidoptera. On the contrary, a few of their features only are given, sufficient to suggest the general structure and appearance of the moths assigned to them.

This will be assisted by reference to the Plates, on which are shown large numbers of species belonging to nearly all the groups mentioned in the text. Moreover, illustrations of one or two characteristic examples of each family are cited in the Tabulation which follows, many of them in their earlier as well as in their imaginal stages. It would thus be a mistake to judge this as a precise classification of the Order. It is rather a guide to the relationships of the moths included in this book.

Taxonomy has suffered from a failure to keep in touch with modern advances in biology. In the Lepidoptera, criteria of the various classificatory divisions are, with but few exceptions, limited to features which can be studied by inspecting small numbers of the early stages and dried specimens preserved in museums. Even the data so obtained have rarely been treated statistically, a quite essential requirement, while genetic, cytological, physiological and chemical methods have hardly yet been used to elucidate the systematics of this Order. In the circumstances, therefore, it is necessary here to employ the conventional standards of classification, while pointing out the necessity of extending them.

The Order Lepidoptera is divided into 3 Suborders, 13 Superfamilies and 64 Families. The butterflies comprise one of these Superfamilies. The remainder of the Lepidoptera are moths, and the species with which this book is concerned belong to 2 of the Suborders, 8 of the Superfamilies and 23 of the Families.

ORDER LEPIDOPTERA

SUBORDER	Homoneura. Neuration of fore- and hind-wings similar. Jugum on fore-wings. No frenulum. Nervure 1c present.
FAMILY	Hepialidae (Swift Moths). Proboscis absent. Maxillary palpi obsolete, the tibiae without spurs. Larva: 10 to 16 prolegs or with the prolegs lost. Pupa: one or two basal abdominal segments fixed. (' Common Swift ': Plate X, figure 6; Plate XVI, figure 1; Plate IX, figure 1; Plate VII, figure 4; ' Ghost Moth ': Plate 28, figures 1 to 5).
SUBORDER	Heteroneura. Neuration of fore- and hind-wings different. Frenulum usually present. Nervure 1c present or absent on hind-wings.
SUPERFAMILY	Caradrinoidea. Maxillary palpi rudimentary or absent. Frenulum present. 1c absent from both fore- and hind-wings. Fore-wings: 5 arises close to 4. Pattern: five transverse lines and three discal spots. Larvae may be very hairy. Usually 10 prolegs, but those on 7th and 8th segments sometimes absent. Pupae with segments 9 to 11 free. Not protruded from cocoon at emergence.
FAMILY	Arctiidae (Tiger Moths). Proboscis more or less developed. Posterior tibiae with all the spurs present. Typical wing markings generally not distinctly traceable. Thorax and abdomen: hairy or smooth beneath. Eggs, spherical and nearly smooth. Larvae, hairy with 10 prolegs.

Pupae, in a cocoon above ground, constructed of silk and larval hairs.
(' Garden Tiger ': Plate 22, figures 1 and 2; Plate 9, figures 5 to 7; ' Muslin ': Plate 10, figures 7 to 10; ' Dingy Footman ': Plate 13, figures 3 and 4).

Family Hypsidae.
Thorax hairy beneath, abdomen smooth.
Proboscis well developed.
Fore and hind-wings: nervure 5 originates near angle of cell.
Eggs spherical, larvae hairy, cocoon very slight.
(' Scarlet Tiger ': Plate XI, figure 4; Plate 15, figure 1).

Family Nolidae.
Proboscis well developed.
Fore-wings with three sub-costal tufts of scales.
Eggs ribbed, larvae with tufts of hair and no prolegs on 7th segment.
Pupae in a boat-shaped cocoon, imagines small.
(' Short Cloaked Moth ': Plate XVI, figure 6; Plate VII, figure 2).

Family Cymbidae.
Proboscis developed.
Many species possess green pigment changed to brown by an alkali.
Larvae with 10 prolegs, not hairy.
Pupae in boat-shaped cocoon.
(' Green Silver Lines ': Plate X, figure 1, Plate 16, figure 1).

Family Caradrinidae (" Noctuid " Moths).
Proboscis usually well developed.
Thorax very hairy beneath.
Hind-wings: nervure 5 absent or imperfect.
Eggs spherical ribbed, or netted.
Larvae with 10 prolegs, usually with few hairs.
Pupae usually subterranean.
About 6,000 species, mainly in temperate regions.
(' Turnip Moth ': Plate 5, figure 5; ' Grey Dagger ': Plate 17, figures 14 and 16; ' Small Dark Yellow Underwing ': Plate 27, figure 15).

Family Plusiidae.
Proboscis well developed.
Fore-wings relatively broader than in Caradrinidae, body more slender.
Hind-wings: nervure 5 well developed.

Eggs spherical, ribbed or netted.
Larvae with few hairs. Sometimes prolegs on 7th or 8th segment absent or rudimentary.
Pupae usually in cocoon above ground.
Principally a tropical family.
('Silver Y': Plate 16, figure 4; 'Red Underwing': Plate 5, figure 1; 'Waved Black': Plate 4, Plate XI figure 2).

Family — Lymantriidae (Tussock Moths).
Proboscis short, generally rudimentary.
Male antennae bipectinated to the tip.
Hind-wings: nervure 5 present.
Eggs spherical and smooth; larvae hairy, with dense tufts.
Pupae hairy, in cocoon above ground.
('Gold Tail': Plate 24, figures 1-4; Plate IX, figures 3 and 4; 'Gispy Moth': Plate 32, figures 3 and 4).

SUPERFAMILY — Notodontoidea.
Maxillary palpi absent.
Fore-wings: 1c absent, 5 no nearer 4 than 6.
Hind-wings: 1c absent. Frenulum nearly always present.
Pupae: segments 9-11 free, not protruded from cocoon on emergence.

Family — Sterrhidae (The Waves).
Proboscis developed.
Fore-wings: 11 connected with 9, 10 springs from 9.
Hind-wings: 5 fully developed.
Eggs oblong and reticulated.
Larvae elongated and slender. Few hairs. Prolegs 7-9 absent.
Pupae in slight cocoon above ground.
('The Blood Vein': Plate 16, figure 5; 'Weaver's Wave': Plate 26, figure 5; 'Portland Ribbon Wave': Plate 26, figure 16).

Family — Geometridae.
Proboscis well developed.
Most species coloured green by a pigment converted to brown by an acid.
Fore-wings: 11 free from 9, 10 arising from 9, 5 fully developed.
Early stages=those of Sterrhidae.
('Common Emerald': Plate 1, figure 4).

Family Hydriomenidae (Carpets and Pugs).

Proboscis well developed.

Fore-wings: 10 arises separately, fusing with 11 and 9, or arises from 11 and fuses with 9, 5 present and fully developed.

Eggs rather flattened and reticulated.

Larvae slender. No prolegs on 7 to 9.

Pupae usually subterranean.

('Mottled Pug': Plate VII, figure 3; 'Marbled Carpet': Plate 13, figures 12-14; 'Water Carpet': Plate 29, figure 8).

Family Brephidae.

Proboscis sometimes developed sometimes degenerate.

Hind-wings: 5 present.

Eggs smooth. Larvae: prolegs on 7, 8 and sometimes 9 rudimentary.

Mainly an Australian family.

('Orange Underwing': Plate 2, figure 6; Plate VII, figure 1; 'Rest Harrow': Plate 3, figure 5).

Family Selidosemidae.

Proboscis usually well developed, sometimes rudimentary.

Fore- and hind-wings: 5 imperfect (not tubular) or absent.

Eggs rather elongated, reticulated or ribbed.

Larvae slender. No functional prolegs on 7, 8 and usually 9.

Pupae subterranean or in slight cocoon above ground.

('Peppered Moth': Plate 19, figure 3; Plate XXIII; 'Scalloped Oak': Plate 8, figures 1 and 2; 'Black Mountain Moth': Plate 27, figures 10 to 12).

Family Polyplocidae.

Proboscis well developed.

Thorax hairy below. Hind-wings: 5 developed.

Eggs netted. Larvae stout; all prolegs developed.

Pupae in slight cocoon above ground.

('Yellow Horned': Plate VIII, figure 2; Plate 25, figure 1.)

Family Sphingidae (Hawk Moths).

Proboscis very long or sometimes imperfect.

Thorax hairy beneath.

Hind-wings: 5 present.

Eggs smooth; larvae stout, usually with posterior horn.

Pupae subterranean.

Imagines large with powerful flight.

	(' Pine Hawk ': Plate XV, figures 1 and 2; Plate 15, figure 2; ' Bee Hawk ': Plate V; ' Striped Hawk ': Plate 3, figure 6, Plate 21, figure 4.)
FAMILY	Notodontidae (the Prominents). Proboscis usually well developed. Imago often with hair-like tuft of scales on inner margin of fore wings. Hind-wings: 5 weak or imperfect. Eggs smooth or pitted. Larvae stout, sometimes without prolegs on 13, usually with humps or tubercles. Pupae usually subterranean. (' Pebble Prominent ': Plate 19, figure 2, Plate 20, figure 2.)
FAMILY	Saturniidae (Emperor and Silk Moths). Proboscis rudimentary. Hind-wings: no frenulum, 1a absent 5 present. Eggs smooth; larvae with tubercles bearing tufts of hair. Pupae in strong oval cocoon of silk. Imagines large. (' Emperor Moth ': Plate 19, figure 1, Plate XI, figure, 1, Plate 18.)
SUPERFAMILY	Papilionoidea (Butterflies).
SUPERFAMILY	Drepanoidea. Maxillary palpi obsolete. Fore-wings: 1c absent. Hind-wings: 1c absent, frenulum present.
FAMILY	Drepanidae (the Hook tips). Male antennae bipectinated. Fore-wings: apex often prolonged into a hook. Hind-wings: 5 close to 4. Eggs pitted. Larvae: no prolegs on 13, anal extremity prolonged and pointed. Pupae in cocoon above ground. (' Pebble Hook-tip ': Plate 2, figures 1 and 3; ' Chinese Character ': Plate 2, figures 2 and 4.)
SUPERFAMILY	Lasiocampoidea. Proboscis rudimentary or absent. Male antennae bipectinated to tip. Maxillary palpi obsolete. Fore-wings: 1c absent; 7, 8 and 9 arise from 10. Hind-wings: 1c absent, no frenulum. Pupae: segments 9 to 11 free, not protruded from cocoon on emergence.

Family	Endromididae. (The characteristics are those of the Superfamily.) Eggs rounded, larvae stout narrowing in front, with few hairs. Pupae in tough cocoon above ground. Imagines large and strikingly coloured. (One British species, the Kentish Glory.)
SUPERFAMILY	Bombycoidea. Proboscis rudimentary or absent. Maxillary palpi obsolete. Fore-wings: 1c absent, 7 separate from 10. Hind-wings: no frenulum, 1c absent.
Family	Lasiocampidae (the Eggars). (The characteristics are those of the Superfamily.) Eggs smooth, larvae very hairy. Pupae in tough cocoon above ground. ('Grass Eggar': Plate 10, figures 3 to 6; 'Lappet': Plate X, figure 2, Plate 6, figure 4).
SUPERFAMILY	Psychoidea. Proboscis present or absent. Maxillary palpi rudimentary (often well developed in pupa). Fore-wings: 1c usually present. Hind-wings: 1c present, the frenulum always developed. Larvae: 10 prolegs, or wholly without prolegs. Pupae: segments 8 to 11 free, protruded from cocoon on emergence.
Family	Heterogeneidae. Proboscis rudimentary or absent. Larvae: short and stout, without prolegs. Pupae: in firm oval cocoon above ground. Imagines: generally small and dull coloured. Mainly a tropical family. ('The Festoon': Plate 2, figure 5; Plate 16, figure 6.)
Family	Zygaenidae (Burnets and Foresters). Proboscis present. Larvae: short and stout, with 10 prolegs. Pupae in strong cocoon above ground. Imagines brightly coloured and day-flying. ('Six-spot Burnet': Plate 24, figures 5 and 6; 'Oban Burnet': Plate 27, figure 9; 'Scarce Forester': Plate 26, figures 11 and 12.)

SUPERFAMILY	Cossoidea. Proboscis absent or rudimentary. Fore-wings: 7 and 8 from one stem, 1c present. Hind-wings with frenulum and 1c present. Eggs smooth. Larvae feed in stems of trees or plants.
Family	Cossidae. (Characteristics are those of Superfamily.) (' Goat Moth ': Plate 6, figure, 1; Plate 5, figure 8.)
SUPERFAMILY	Tinaeoidea. Maxillary palpi usually developed. Fore- and hind-wings: 1c present. Neuration often much reduced. Frenulum present.
Family	Sesiidae (The Clearwings). Antennae generally dilated towards tip. Wings usually scaleless in part. Fore-wings elongated and narrow. Hind-wings, 5 absent. Larvae with 10 prolegs, feed in stems of trees or roots of plants. Pupae in larval gallery, protruded from cocoon on emergence. (' Hornet Moth ': Plate 25, figure 4; ' Clear Underwing ': Plate 29, figure 10; ' Red-belted Clearwing ': Plate XVI, figure 2.)

GLOSSARY

(*All references to climate apply to the British Isles only*)

Allelomorphs. A pair of genes controlling the same character, or set of characters. Their members are derived respectively from the two parents and segregate into separate reproductive cells.

Anal angle. The corner of the hind-wing nearest the posterior end of the body (=*tornus* of hind-wing).

Androconia. Scales specialised for distributing the attractive scent of the male.

Antennæ. The long pair of feelers on the head of a butterfly or moth. They are appendages, and are sensory in function.

Apex. The tip of the fore- or hind-wings, at that end of the costa which is farthest from the body.

Appendages. Jointed limbs, originally one pair to each segment and used for walking. Some have later been modified to form jaws and other organs.

Autosome. Any chromosome other than a sex-chromosome.

Back-cross. A mating between a heterozygote and a homozygote. It leads to segregation in equality.

Buffer. A substance which confers stability on a solution. (In physiology, one which prevents the reaction of a solution from changing on addition of acid or alkali.)

Cells. Microscopic units into which protoplasm is divided.

Cells of wings. The central area of the wing surrounded, but not crossed, by nervures.

Chitin. Horn-like substance forming the external covering of insects.

Chlorophyll. The green pigment of plants.

Chromosomes. Thread-like structures present in pairs (called *homologous chromosomes*) in every cell of the body. There is usually a fixed number of them in each species, and they carry the genes.

Claspers (*adult*). Part of the male genital organs: a pair of modified appendages at the end of the body by which the female is held during copulation.

Claspers (*larval*). The pair of " prolegs " at the hind-end of a caterpillar's body.

Cline. A character-gradient, in which the structure or physiology of an organism changes more or less gradually over a given area.

Cocoon. A case enclosing and protecting a pupa. It is made of silk, often strengthened with other materials.

Costa. The front edge of the fore- or hind-wings.

Cremaster. Arrangement of hooks at the end of the body by which a pupa is attached to its support. The hooks are entangled in a pad of silk spun by the larva.

Crossing-over. The exchange of corresponding segments between chromatids derived from different but homologous chromosomes. This involves two members out of the two pairs that are available in a diploid at any one position.

Cross-over Value. The frequency of crossing-over between two genes, calculated as the sum of the two recombination classes of a back-cross expressed as a percentage of the total.

Cryptic colours. Those which help to conceal an animal by making it resemble its surroundings.

Dominant. A character which is fully developed when the genes controlling it are in either the heterozygous or the homozygous state (compare *recessive*).

Ecdysis. The moulting of the chitinous cuticle of an insect.

Ecology. The relation of animals and plants to their environment.

Entomology. The study of insects.

Euryplastic species. Those with a wide range of tolerance to environmental conditions. They may adjust themselves to diversity by appropriate variation or by a high degree of plasticity.

F_1. The first filial generation.

F_2. The second filial generation.

Factors (*hereditary*). The hereditary units which control the development of definite characters. They are present in pairs, the members of which are separately called *genes* and, together, *allelomorphs.*

First filial generation. The offspring of a given mating.

Flavones. Non-nitrogenous plant pigments responsible for a range of colours from ivory to deep yellow.

Frenulum. A coupling apparatus uniting the fore- and hind-wings of moths, but not butterflies, during flight.

Gametes. The reproductive cells.

Ganglion. A swelling on a nerve due to the presence at one place of the nuclei of the nerve-cells.

Gene-complex. The interacting system produced by the whole of the hereditary factors of an organism.

Genes. The members of a pair of hereditary factors. They are responsible for the production of definite characters.

Genetics. The study of variation and hereditary.

Genitalia. The external organs of reproduction.

Germ-cells. Those destined to produce the reproductive cells: the sperm and the egg.

Gland. An organ manufacturing substances of use to the body (secretions). They are normally passed down a tube (duct) to the place where they are required.

Gland, ductless. One which passes its secretions directly into the blood; these secretions are called hormones.

Gynandromorph. A sexual abnormality in which male and female parts develop simultaneously, due to an incorrect distribution of the X-chromosomes in the cells of certain tissues (compare *intersex*).

Hermaphrodite. Any individual in which the two sexes are combined.

Heterozygote. An individual in which the members of a given allelomorphic pair of genes are dissimilar.

Hibernation. A quiescent state in which some animals spend the winter.

Holocene period. Recent geological times, since the last ice-age.

Homozygote. An individual in which the members of a given pair of allelomorphs are alike.

Hormone. The product of a ductless gland which, when discharged into the blood, affects a distant part of the body.

Humeral lobe. A projection from the basal part of the costa of the hind-wings. It helps to keep the fore- and hind-wings of butterflies together during flight, by increasing the overlap between them.

Imago. The perfect insect, after emergence from the chrysalis.

Inner margin. The posterior edge of the fore- and hind-wings.

Instar. The form assumed by an insect between each ecdysis: the imago, the pupa, and the phase between each larval moult.

Intersex. A sexual abnormality in which an animal develops first as one sex and later as the other. It is due to an incorrect balance between the male and female-determining genes (compare *gynandromorph*).

Larva. A caterpillar.

Lepidoptera. Butterflies and moths.

Linkage. The tendency for genes to remain together, instead of segregating independently, because they are carried in the same chromosomes.

Lumen. A unit of luminosity. One lumen $= 1.496 \times 10^{-3}$ watts. 12.57 lumens = one spherical candle-power.

Malpighian tubules. The excretory organs of insects. They open into the alimentary canal.

Mandibles. The jaws: present in the larva, atrophied in the imago.

Maxillæ. In primitive insects, a second pair of jaw-like structures behind the mandibles. They are degenerate in butterfly larvæ, and modified into the long sucking proboscis (" tongue ") of the imago.

Melanin. Black, brownish, or dull red animal pigment containing nitrogen.

Mendelian heredity. Responsible for nearly all organic inheritance. The characters are determined by pairs of hereditary units (genes) received respectively from the two parents. The genes are very permanent, neither frequently changing (mutating) nor contaminating one another.

Mesothorax. The middle of the three segments of which an insect's chest (thorax) is formed. It bears a pair of legs and the fore-wings.

Metabolism. The life-processes of the body. Building up protoplasm from food, and breaking down compounds with release of energy.

Metamorphosis. A sudden alteration in form, without growth: the change from larva to pupa, or pupa to imago.

Metathorax. The last of the three segments of which an insect's chest is formed. It bears a pair of legs and the hind-wings.

Micropyle. The minute opening in the chitinous shell of the egg, through which the sperm enters.

Mutation. The inception of a heritable variation, due to a change in a unit of inheritance.

Neolithic culture. That of the New Stone Age, *c.* 2500-2000 B.C. or slightly later. The beginning of material civilisation, produced by men who grew corn and domesticated animals.

Nervures. The struts supporting the wings of insects.

Ocelli. Eyes of simple structure found in larvæ and, rarely, on the top of the head in adult Lepidoptera.

Oesophagus. The gullet, or first part of the alimentary canal, leading back from the mouth.

Outer margin. The edge of the fore- and hind-wings farthest from the body.

Ovipositor. The structure with which the eggs are laid.

Palpi. Pair of short sensory feelers belonging to the mouth-parts and attached below the head.

P_1 generation. The first parental generation, individuals of which are mated to produce a given cross.

Pleistocene Period. Series of glacial and inter-glacial eras previous to recent (Holocene) times. The period of the great ice-ages.

Polygenes. Genes which have small, similar, and additive effects tending, therefore, to produce continuous variation. They are usually widely scattered on the chromosomes, and there may be many polygenic systems in an organism.

Polymorphism. The occurrence together in the same habitat of two or more discontinuous forms of a species, the rarest of which is too frequent to be maintained merely by recurrent mutation.

Precostal nervure. That supporting the humeral lobe.

Prolegs. Legs belonging to the abdominal segments of the larva. They are absent from the imago.

Prothoracic legs. Those belonging to the first segment of the chest (thorax). They are degenerate in some families, fully-formed in others.

Protoplasm. The living substance of the body.

Pupa. A chrysalis.

Pupation. The formation of the pupa by metamorphosis.

Recessive. A character which is developed only when the genes controlling it are homozygous (compare *dominant*).

Recombination. The reassortment of genes, produced by segregation.

Scales. Flat microscopic structures of chitin covering the body and wings of butterflies and moths. They contain pigment and are responsible for the colours of these insects.

Second filial generation. The grandchildren of an original cross, produced by mating together brother and sister of the F_1 generation.

Secretions. Substances of use to the body, manufactured by glands.

Segregation. The separation from one another of the pairs of genes constituting the allelomorphs, and their passage respectively into different reproductive cells.

Setæ. Structures resembling hairs, but formed of chitin.

Sex-chromosomes. The X and Y-chromosomes.

Sex-controlled inheritance. That due to genes, situated in any chromosome, which produce their effects in one sex only, though transmitted by both.

Sex-linkage. The association of characters with sex, because the genes controlling them are carried in the sex-chromosomes.

Specific modifiers. Genes which modify the effect produced by other genes. They may be without effect by themselves.

Sperms. The male reproductive cells.

Spiracles. Paired openings on the sides of insects, leading into the tracheal tubes.

Stenoplastic species. Those that are accurately adjusted to particular environmental conditions and, consequently tend to be very constant.

Tarsus. The foot; typically of five joints in Lepidoptera, but it may be much reduced.

Tergum. The chitinous plate forming the dorsal side of each segment.

Thorax. The chest; composed of three segments. Each has a pair of legs, and the two last a pair of wings.

Tibia. The shin; it is immediately above the foot.

Tornus. The angle of the wings between the outer and inner margins; on the hind-wings often called the *anal angle.*

Tracheal tubes. The respiratory tubes of insects.

Tracheoles. The very fine ends of the tracheal tubes.

Warning colours. Those which make an animal conspicuous, and advertise that it is protected by a nauseous taste or other means.

X-chromosomes. The chromosomes carrying the genes which control sex-determination.

Y-chromosome. The partner of the X-chromosome in one of the two sexes: the female in Lepidoptera. It contains but few genes and, in general, does not control sex-determination.

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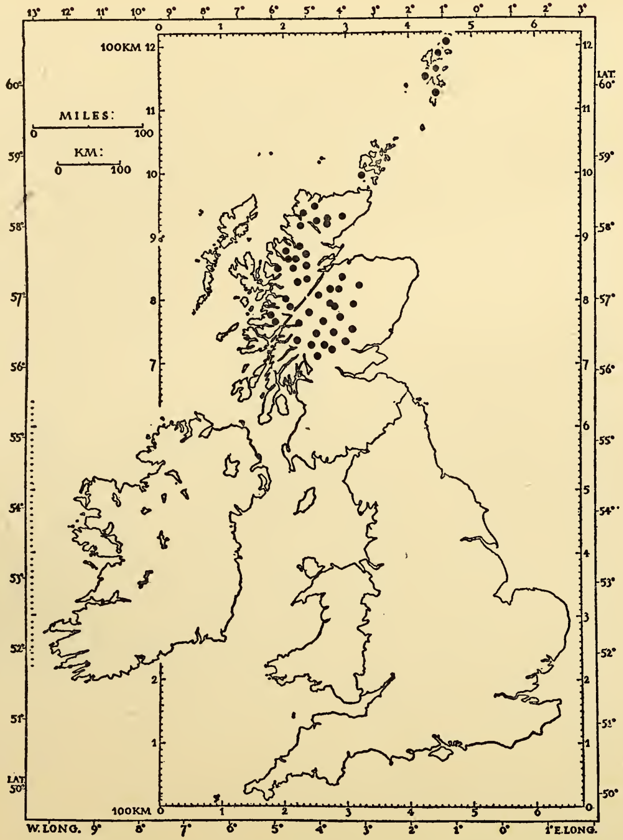
Descriptions of the moths referred to in this book, together with information on their times of appearance and distribution, may be obtained from Meyrick (1927) and South (1939). The latter work illustrates nearly all the imagines in colour, and those species discovered since its first publication in 1907 are discussed in an Appendix to each volume of the third Edition. Stovin describes the caterpillars in more detail, but his account is based upon that of South.

MAPS SHOWING
THE DISTRIBUTION OF CERTAIN MOTHS IN THE BRITISH ISLES

THE FOLLOWING MAPS illustrate certain aspects of distribution:

Ice Age Relicts (Numbers 1 and 2), Interglacial Relicts (Numbers 3 to 6), of which Numbers 5 and 6 are adjusted to coastal conditions, three extremely localised species (Number 7), a species limited to chalk or calcareous soil (Number 8), a Holocene colonist or Interglacial Relict adjusted to coastal conditions (Number 9), Holocene colonists (Numbers 10 to 12).

These include also several instances of discontinuous distribution, see especially Numbers 3 and 6.


MILES:
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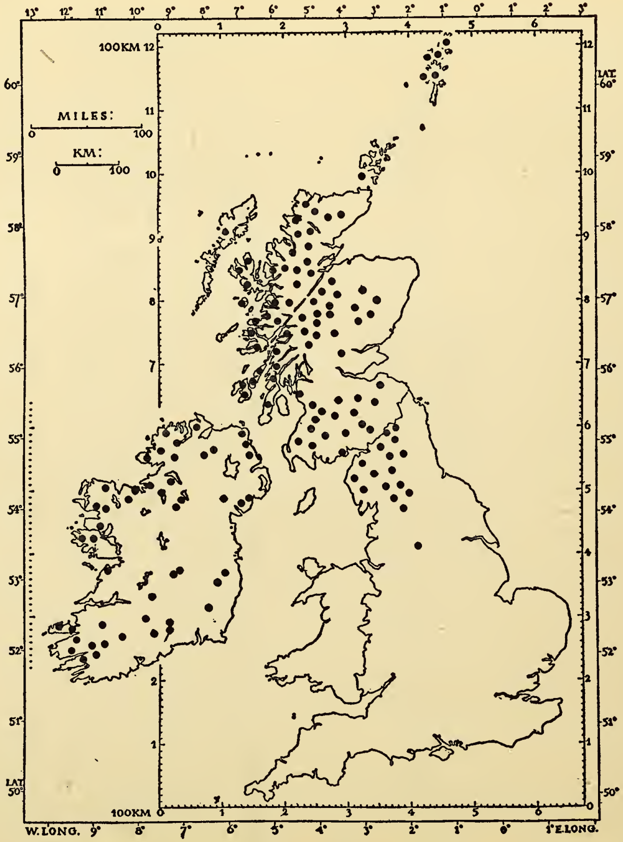
LAT.

1. Broad-bordered White Underwing, *Anarta melanopa*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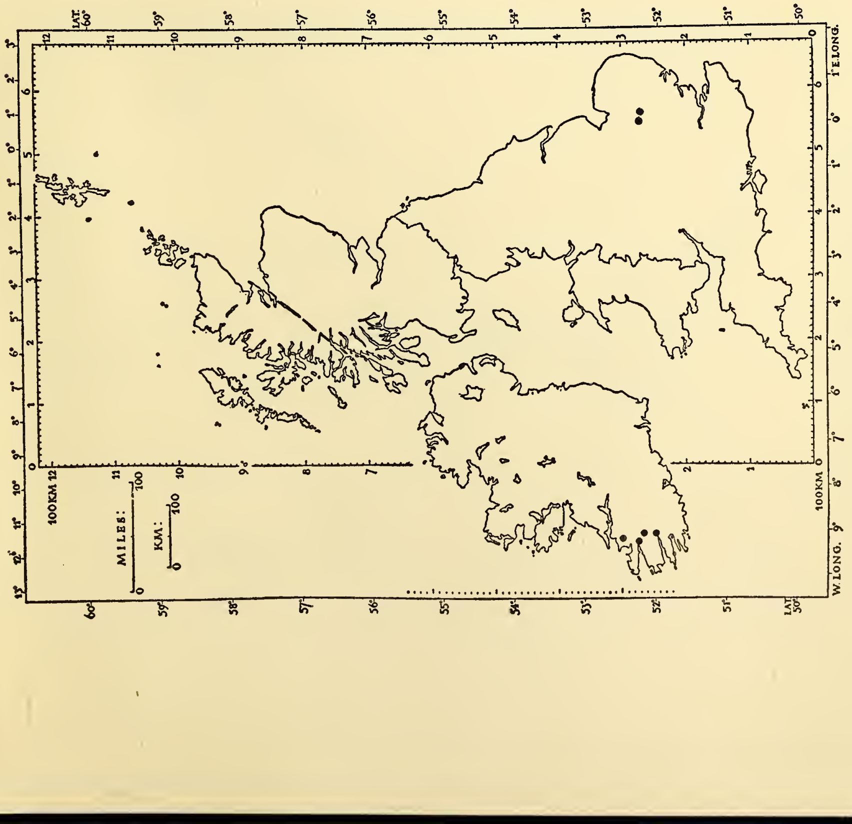
LAT.

2. Grey Mountain Carpet, *Entephria caesiata*


LAT. 60°
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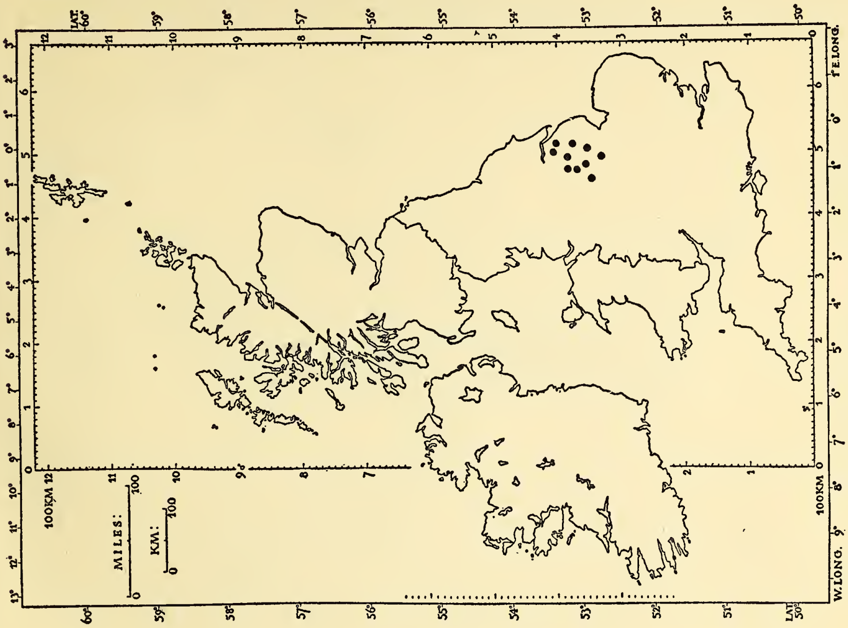
W. LONG.
1° E. LONG.

3. The Silver Barred, *Eustrotia olivana*


LAT. 60°
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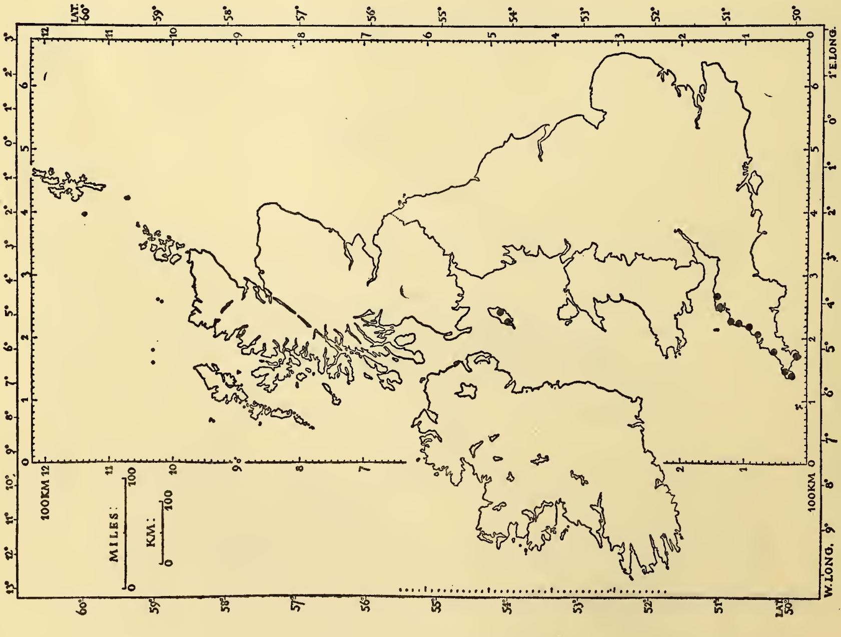
1° E. LONG.

4. Union Rustic, *Apamea pabulatricula*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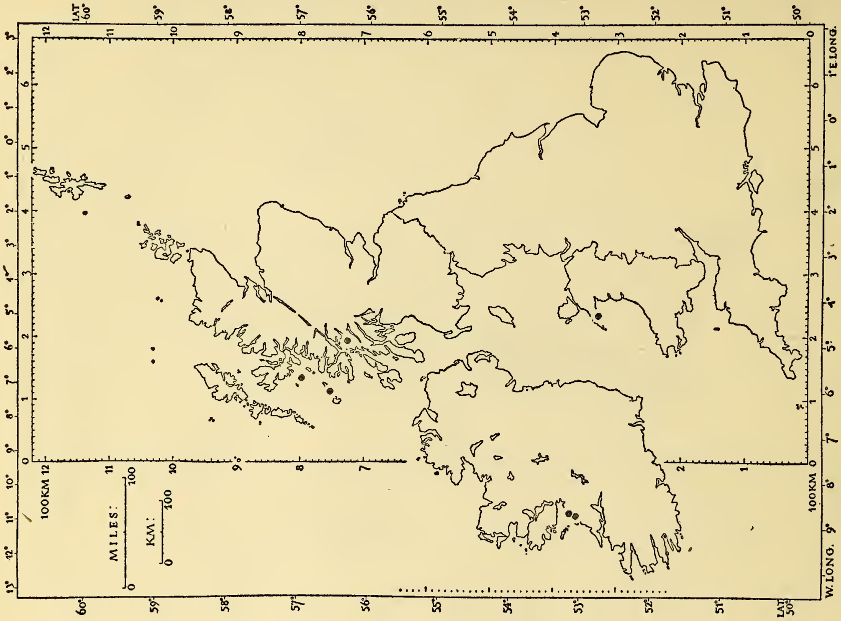
LAT.

5. Black-banded, *Antitype xanthomista*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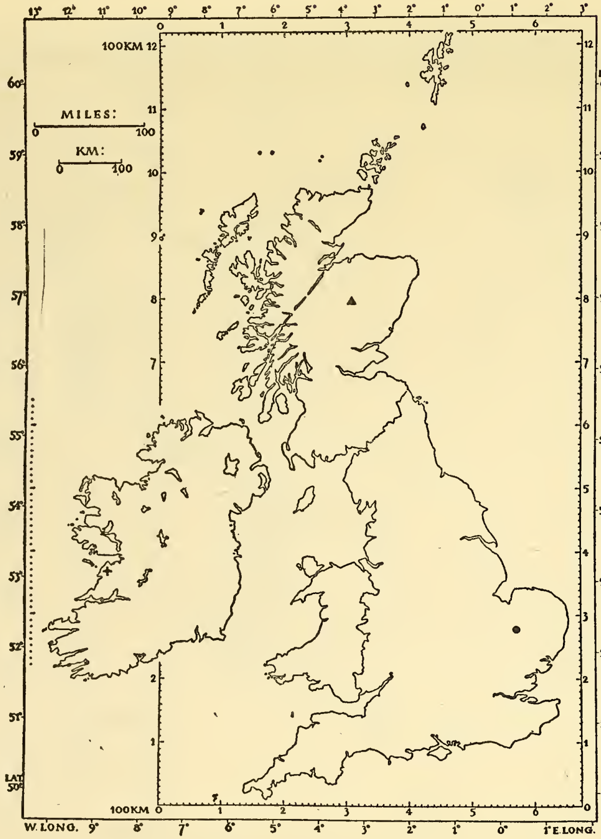
LAT.

6. Transparent Burnet, *Zygaena purpuralis*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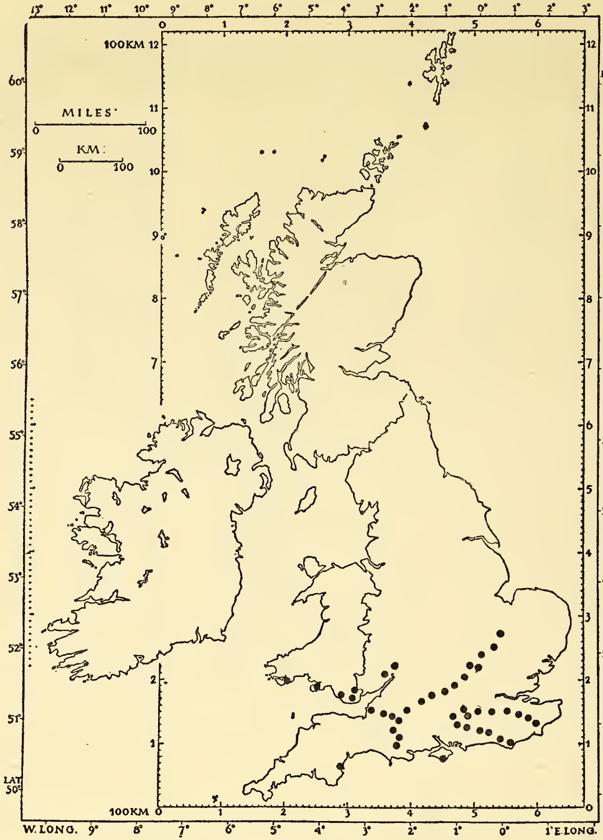
100KM 12
LAT 60
W. LONG.
1° E. LONG.

7. + *Calamia virens.* ▶ Mountain Burnet, *Zygaena exulans.* ● The Viper's Bugloss, *Anepia irregularis*


MILES·
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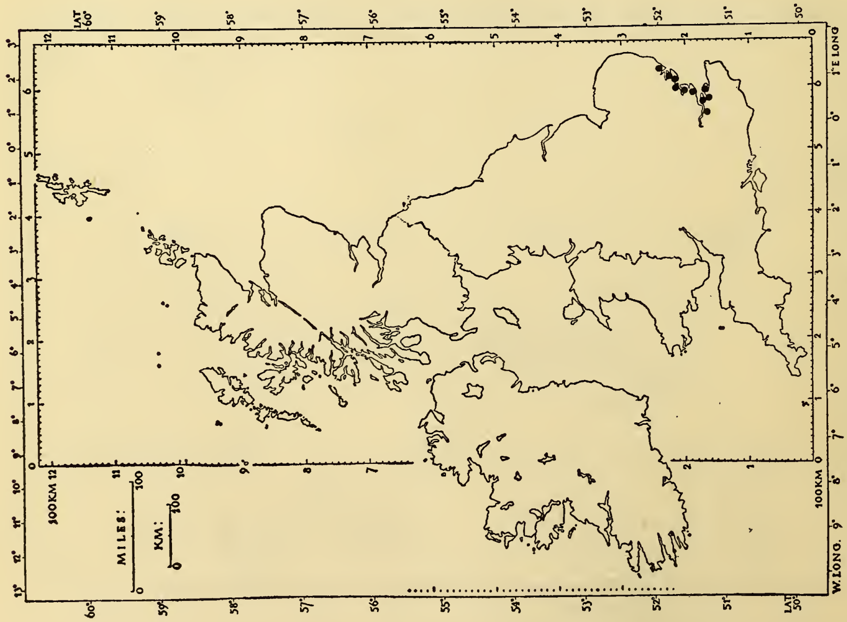
100KM 12
LAT 60°
W. LONG.
1° E. LONG.

8. Chalk Carpet, *Ortholitha bipunctaria*


MILES
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KM
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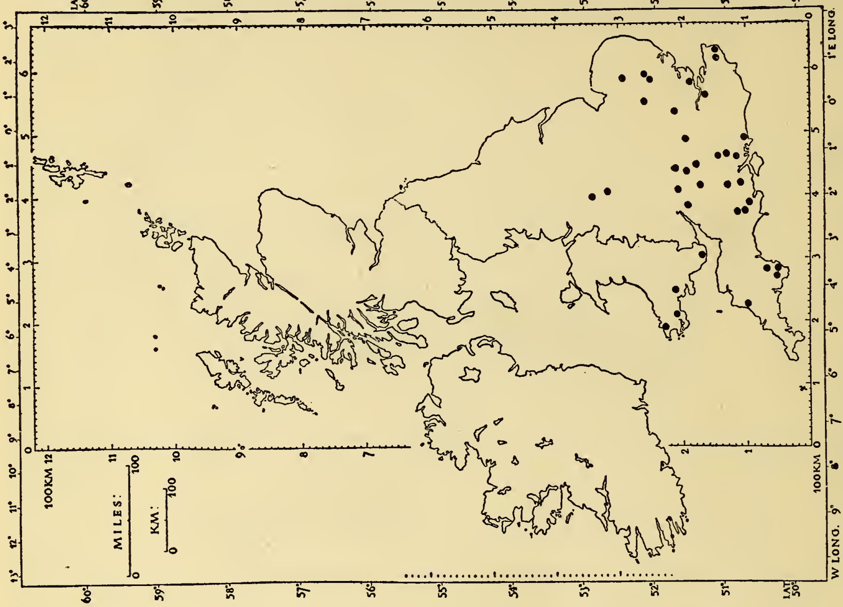
W LONG.
1° E LONG
LAT 60°
LAT 50°
100 KM

9. Ground Lackey, *Malacosoma castrensis*


MILES
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KM
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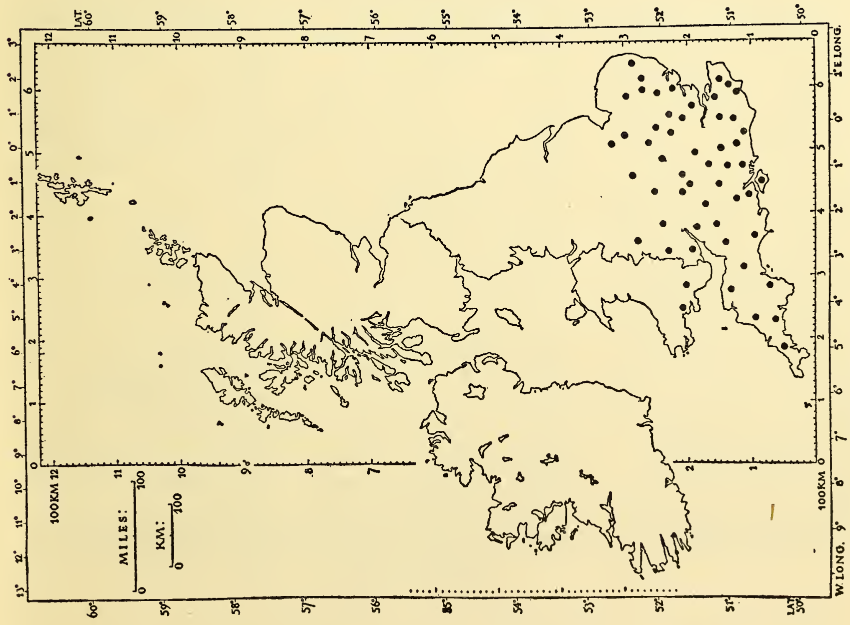
W LONG.
1° E LONG.
LAT 60°
LAT 50°
100 KM

10. Scarlet Tiger, *Panaxia dominula*


LAT. 60°
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E. LONG.
100 KM
MILES: 0 100
KM: 0 100

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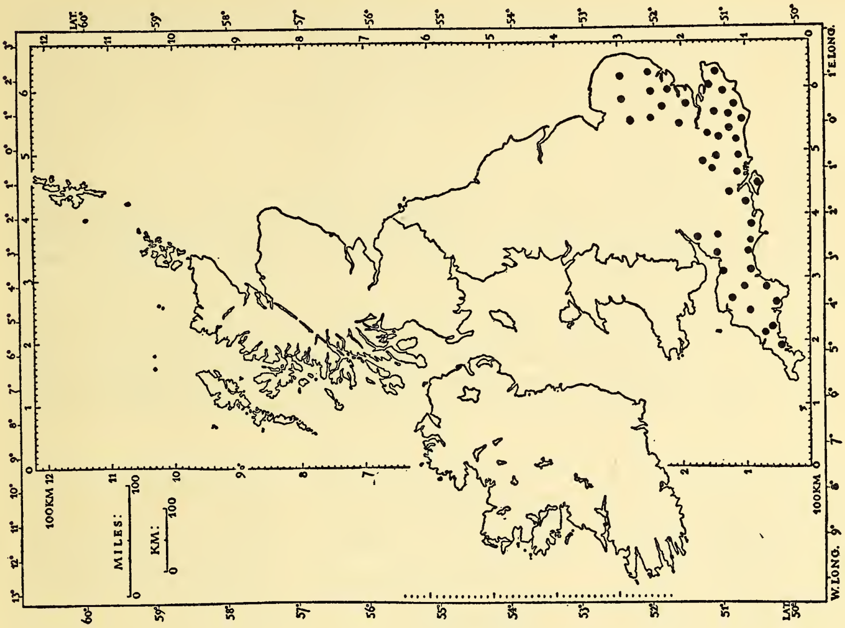
LAT. 60°
W. LONG.
E. LONG.
100 KM
MILES: 0 100
KM: 0 100

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The moths are indexed under their English names, with cross-references both from the full scientific name (generic and specific) and from the specific name only. Those species without an English name are indexed under the full scientific one, with a cross-reference also from the specific name. Food plants and localities are entered only if of special interest and significance. The Glossary and Bibliography, being themselves alphabetically arranged, are not indexed.

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